PELAGIC *SARGASSUM* AND ITS ASSOCIATED MOBILE FAUNA IN THE CARIBBEAN, GULF OF MEXICO, AND SARGASSO SEA

A Thesis

by

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ABSTRACT

There are many species of the genus *Sargassum* distributed in tropical and subtropical waters but only two, *S. natans* and *S. fluitans*, have an entirely pelagic life cycle and offer ecologically-supportive structures of different forms in otherwise nutrient-poor environments. *Sargassum* represents a keystone species supporting relatively high levels of biodiversity which is required for the maintenance of the health and resilience of a unique ecosystem currently facing many anthropogenic pressures. While studied for years, no simultaneous comparisons have been performed between the three regions in which *Sargassum* is most commonly found: the Gulf of Mexico, Caribbean, and Sargasso Sea. Dip-net *Sargassum* samples and associated macrofauna were collected from these three regions during the Spring/Summer of 2015 to examine differences in *Sargassum* species, structure, and faunal distribution. An unusually large abundance of the rare form *S. natans VIII* was seen in all three regions in addition to the more common forms of *S. natans I* and *S. fluitans III*. Isolated clumps and rows of *Sargassum* were equally common in all three regions while mats were comparatively rare. *Sargassum* from the Gulf, Caribbean, and Sargasso Sea shared five common (frequency >10%) species. Differences in the physical forms of *Sargassum* forms had a marked effect on fauna diversity and abundance. In all three regions, fewer individuals and species were found on the broad-leafed, less compact *S. natans VIII* than on the denser *S. natans I* and *S. fluitans III*. The majority of these species are benthic-like species that physically require the *Sargassum* substrate (unlike most fish), and therefore likely avoid loose *S. natans VIII* which offers less surface area and protection from

predators. This study identifies the differences in macrofauna abundance and diversity between varieties of *Sargassum* and highlights the potential for dramatic community assemblage changes that could result from largescale *Sargassum* blooms and species shifts.

DEDICATION

To my family

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TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

Page

I. INTRODUCTION

There are many species of the genus *Sargassum* distributed throughout tropical and subtropical oceans but only two, *Sargassum natans* and *Sargassum fluitans*, have an entirely pelagic lifecycle. Presence of pelagic *Sargassum* in oligotrophic waters of the Caribbean, Gulf of Mexico, and Sargasso Sea means that even small pieces of *Sargassum* act like magnets for a wide variety of fauna. For these fauna, which range from epibionts like hydroids, to clinging fauna like crabs, to free-swimming species like filefish, pelagic *Sargassum* may serve as primary habitat, temporary refuge, foraging habitat, or nursery ground. Variation in blade size and shape, number of floats, and general branching and arrangement has led to the recognition of distinct forms within each species of pelagic *Sargassum* (Parr 1939). These morphological differences may dictate habitat value for the associated faunal community. Therefore, differences in faunal communities are expected among different *Sargassum* forms. Because mobile fauna provide a direct link to migratory species that use the mats as a foraging habitat, differences in mobile fauna communities could lead to differences in the success of migratory fauna, like turtles and eel larvae, that depend on *Sargassum* fauna as a food source. Furthermore, given the wide distribution of pelagic *Sargassum* throughout the North Atlantic and adjoining seas, a geographic difference in associated faunal community is also expected.

Sargassum *Species, Form, & Aggregation Patterns*

Commonly known as "Gulf weed," pelagic *Sargassum* was originally described by Carl Linnaeus in 1753 (Linnaeus, 1753) but it was subsequently transferred to the

genus *Sargassum* by Benjamin Gaillon in 1828 (Gaillon 1828). The genus *Sargassum* is a multicellular alga with firm but flexible stipes supporting branching globular gas-filled bladders and leafy fronds. Healthy bladders allow the plant to stay upright in submerged conditions and, in the case of *S. natans* and *S. fluitans,* remain afloat on the surface in the neuston environment where water column irradiance is at a maximum. While the majority of benthic specimens are generally dark brown or green in color, pelagic species are a vivid gold, standing out against a deep blue background of the open ocean. Unlike benthic specimens, *S. natans* and *S. fluitans* reproduce asexually through continued budding and breaking off of segments known as thallus fragmentation (Kilar, Hanisak, & Yoshida 1992) although one instance of reproductive structures present on unattached, pelagic *Sargassum* has been reported (Moreira & Suarez 2002). While *S. natans* and *S. fluitans* are genetically distinct species (Camacho et al 2015; Olsen and Tonkin 2015), little research concerning pelagic *Sargassum* genetics has been published meaning that the degree to which these apparent clones and their morphological forms are related is, as yet, unknown.

While there are only two species of pelagic *Sargassum,* each species consists of several morphological forms. These forms, best described by Parr (1939) and Winge (1923), also differ in abundance. The most common form of *S. natans* is *S. natans I* which is characterized by small, narrow blades, narrow branching stipes, and spiked bladders (floats) half as numerous as blades. In contrast, *S. flutians III,* the most common form of *S. fluitans*, displays higher order branching with dense foliation and bladders typically more numerous than blades. The stipes of this form are covered in small thorns

(<1mm) which are most visible on the distal growth region which have yet to become covered with encrusting fauna. Because few modern studies have distinguished between *Sargassum* species or forms, abundance estimates for typically rare forms are not available. One rare form is *S. natans VIII* which is characterized by broad blades, an open habitus, and thick stipe. *S. natans VIII* can often only be distinguished from *S. fluitans III* by its complete lack of thorns on the stipe and rare occurrence of spikes on bladders (Schell, Goodwin, & Siuda 2015) (Figure 1).

While the two species differ genetically (Comacho et al 2015, Olsen & Tonkin 2015), no data concerning genetic distinction between morphologically unique forms exist. Both species that coexist in pelagic waters can often be found floating directly next to each other. Despite these shared characteristics, individual colonies of *Sargassum* forms differ greatly in terms of their structural complexity, an increase in which has been connected to an increase in species diversity (Huffaker 1958). Even in close association, fine-scale habitat variation resulting from these distinct morphological differences might lead to variation in associated fauna. Because they are difficult to track, the origins and drift patterns of pelagic *Sargassum* have always been uncertain. Remote satellite sensing techniques, which cannot distinguish *Sargassum* species, suggest that drifting *Sargassum* is moved through the oceans by surface currents and winds on an annual cycle that is thought to begin in the Gulf of Mexico during spring and ends in the southern Sargasso Sea during the following winter (Gower & King 2011) (Figure 2).

Figure 1: Specimens of *S. fluitans III*, *S. natans I*, and *S. natans VIII* showing large and small-scale morphological differences. Large-scale includes branching patterns while small-scale includes the presence or absence of thorns on stems and spines on bladders as well as blade length and width. Reprinted from Schell, Goodwin, & Siuda (2015) with permission.

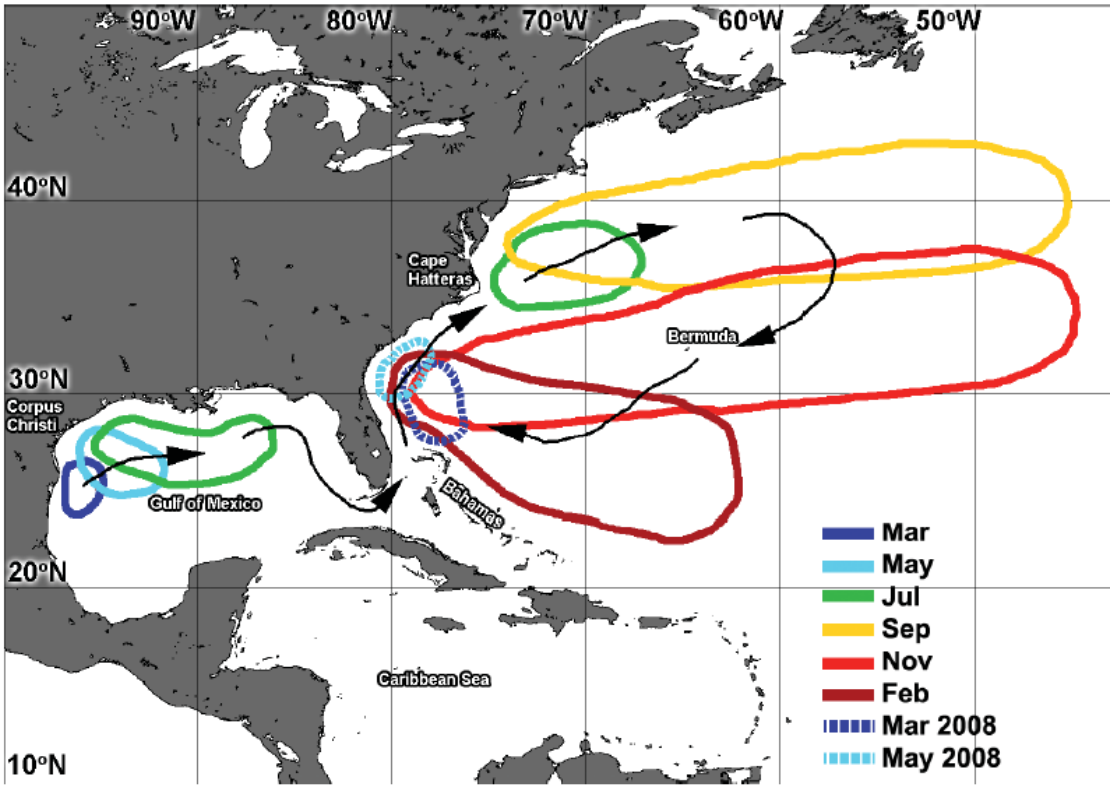

Figure 2: From Gower & King (2011) with permission, showing MERIS detected *Sargassum* distributions over the course of approximately one year shows large accumulations of the algae moving from the Gulf in the spring and early summer to the northern Sargasso Sea in the fall, moving towards the south in the late fall to winter. In 2008, an anomalously large quantity of *Sargassum* was detected off the coast of Florida.

However, direct sampling from the Florida Straits, Sargasso Sea, and Caribbean Sea suggests that only *S. fluitans* follows this cycle, repopulating the Gulf of Mexico by transport through the western Caribbean (Goodwin, Schell, & Siuda 2014). *S. natans I* is most abundant and found year round in the Sargasso Sea (Goodwin, Schell, & Siuda

2014) and, with *S. fluitans*, experiences a north to south shift from the fall to the spring (Figure 3). During both seasons, a spatial division between *S. fluitans* and *S. natans* remained constant with the later remaining further north of the former. Strict identification of forms was not conducted during this field sampling and so the presence of typically rare forms may have gone unnoticed. Significant pelagic *Sargassum* presence in the eastern Caribbean was only noted during 2011, a year of large blooms. While *S. fluitans III* and *S. natans I* have remained the most common of Parr's forms since their classification, other forms are occasional found although rarely in any significant abundance. One such form is *S. natans VIII* which is thought to be sourced from the North Equatorial Recirculation Region (NERR) (Johnson et al 2012, Schell, Goodwin, & Siuda 2015) from which it travels through the Caribbean, to the Gulf of Mexico and/or, theoretically, to the Sargasso Sea.

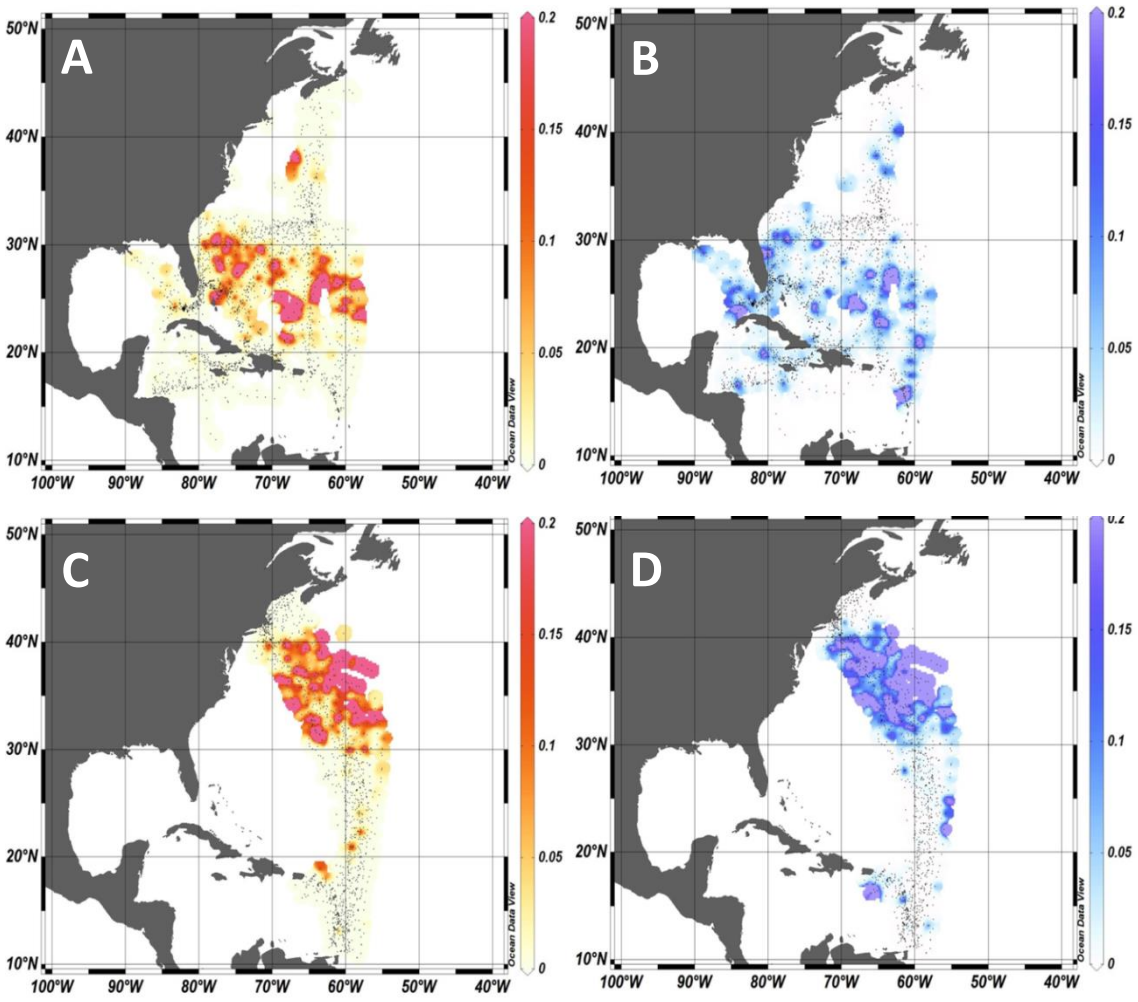

Figure 3: Distribution of *Sargassum* in the Sargasso Sea (g/m^2) (1992-2013) shows seasonal shift. (A) *S. natans*, spring, (B) *S. fluitans*, April – early June, (C) *S. natans*, late October – early November, (D) *S. fluitans*, fall (Goodwin, Schell, & Siuda 2014, with permission). Forms were not specifically identified during this collection period.

Depending on sea surface currents and wind conditions, drifting pieces or colonies of *Sargassum* are typically found as isolated colonies or clustered into windrows or large mats. Mats hundreds of meters across, like those described by early

sailors including Christopher Columbus in the Sargasso Sea (Dickinson 1894), are the result of converging surface currents in areas of downwelling and low winds. Positively buoyant material, like *Sargassum* accumulates where convective cells converge. Windrows, lines of *Sargassum* only 0.5-1 meter across but hundreds of meters long, arise from Langmuir circulation (Langmuir 1938). These rows contain a greater area of connected habitat compared to isolated clumps. As a result, these clumps may display similar effects as anthropogenically fragmented habitat albeit on a more rapidly shifting timescale. As a result of fragmentation, smaller patches (i.e. an isolated clump) support fewer species per unit area than the same unit of area in a larger patch (i.e. a windrow) (Hansski & Simberloff 1997, MacArthur & Wilson 1967). Under moderately strong, steady wind conditions, series of slowly counter-rotating vortices just beneath the ocean's surface aggregate floating surface material, like *Sargassum*, into lines running parallel to the wind. In high wind and sea state conditions, surface clusters like mats and windrows break apart leaving isolated clumps of *Sargassum* floating on the surface. This vigorous wave action often results in decayed regions of algae, which lack viable floats, breaking off from growth regions and sinking through the water column. Decaying floats are not the only mechanism by which *Sargassum* colonies sink. Floats on healthy algae, when submerged too deep, will collapse under pressure, causing the algae to sink (Parr 1939). The impact of environmental parameters on individual colony condition and, therefore, habitat size may subsequently impact each group of associated fauna.

Sargassum *Fauna*

Fauna associated with *Sargassum* are wide ranging in size and age class as well as morphology (Bortone et al 1977, Fine 1970, Hoffmayer el al 2005, Huffard et al 2014). *Sargassum* is home to several endemic species including but not limited to *Sargassum* frogfish (*Histrio histrio*), *Sargassum* pipefish (*Syngnathus pelagicus*), and multiple species of shrimp (*Latreutes fucorum, Leander tenucornis,* and *Hippolyte coerulescens*) (Butler et al 1983, Coston-Clements et al 1991), which spend their whole adult lives among the weed. Benthic mobile species like crabs, shrimp, snails, polychaete worms, flatworms, and nudibranchs are also found in abundance. Epifauna or non-mobile benthic fauna like tubeworms and bryozoans can be found in large densities on sections of older *Sargassum*. In addition, the algae provides temporary shelter for pelagic fish like jacks (*Carangidae*), juvenile American and European eels (*Anguilla rostrate* and *A. Anguilla*), mahi mahi (*Coryphaena equisetis*), and for juvenile sea turtles (Casazza & Ross 2008). For many endangered or threatened species of sea turtles, *Sargassum* represents a vital habitat during their juvenile life stage termed the "lost years" (Whitherington et al 2012). Like young turtles, passing seabirds also use large mats to rest (Haney, 1986). With plenty of prey available, large *Sargassum* aggregations rapidly attract apex predatory species like marlin, tuna, and sharks during early and mature life history stages (Rooker et al 2006, Wells & Rooker 2004). Scientists and lawmakers have recognized the importance of this habitat, resulting in a ban of commercial harvest of *Sargassum* within U.S. jurisdictional waters by the National Marine Fisheries Service in 2003 (South Atlantic Fishery Management Council 2002).

The nature of drifting *Sargassum* means that even studies outside of the region still contribute in a very real way to the conservation plans for nearby regions like that being attempted by the Sargasso Sea Commission starting with the signing of the Hamilton Declaration in 2014 by representatives of the governments of Bermuda, the Azores, Monaco, the United Kingdom, and the United States of America. Because of pelagic *Sargassum,* a diverse and prolific community is able to exist in what are typically nutrient-poor, oligotrophic waters.

Threats to Sargassum

In oligotrophic central gyres, regions that offer little to sustain life, *Sargassum* represents a foundation species, supporting relatively high levels of biodiversity compared to the surrounding waters. The preservation of high biodiversity is required for the maintenance of the health (Daily 1999) and resilience (Walker 1995) of an ecosystem. Not only is *Sargassum* an oasis in desert-like conditions, it also benefits land habitats when it is washed ashore by prevailing currents and winds. In moderation, *Sargassum* on beaches has been shown to act as a fertilizer, increasing available nutrients (Williams & Feagin 2010) as well as preventing erosion (*Sargassum* Early Advisory System Report 2014, Webster et al 2007). This important habitat, however, is currently under threat, facing a multitude of anthropogenic pressures including harvesting, shipping traffic, oil spills, and climate change (summarized in Laffoley et al 2011). Because of the amount of biodiversity *Sargassum* supports, harvesting it directly from the ocean is akin to clearcutting a forest. Especially after the Deepwater Horizon oil spill, the negative impact of oil on *Sargassum* communities became apparent. A study

by Powers et al (2013) showed that the varied morphologies of *S. natans* and *S. fluitans* (unknown forms) responded differently (time to sinking) to the presence of oil, dispersant, and oil with dispersant.

While the effects of oil spills and subsequent cleanup efforts on pelagic *Sargassum* may be significant, they are far less prevalent than the blooms occurring in the southern portion of its range. In this case, *Sargassum* and the community it supports are not only under threat from a rapid ecological shift but the alga itself is also threatening a variety of other organisms, habitats, and human populations. A massive bloom representing a nearly two hundred-fold increase from the 22 year average was observed in 2011 ranging from Trinidad to the Dominican Republic and across the Atlantic as far as Ghana (Gower et al 2013, Schell, Goodwin & Siuda 2015). In 2014, a localized large-scale bloom off the coast of Texas severely affected the Galveston beach system and endangered turtle nesting grounds. During a single day of the inundation (May 22, 2014), a record 8,400 tons washed ashore on one three-mile stretch of beach (*Sargassum* Early Advisory System 2014). Reports from the Sea Turtle Restoration Project in Galveston, TX of dead sea turtles found in washed up *Sargassum* were also more numerous than usual during this time (Rice June 14, 2014). Multiple endangered Kemp's Ridley sea turtles were found dead on *Sargassum*-covered beaches. Adult female turtles that could make it to their nesting beaches often had nests destroyed as a result of bulldozing cleanup efforts.

According to local news sources (Lum January 29, 2015) and reports by the University of Southern Mississippi's Gulf Coastal Research Laboratory and Schell,

Goodwin, & Siuda (2015), another massive atypical bloom occurred in the southeastern Caribbean throughout 2015, sourced from the NERR. Blooms in this region not only deter tourism, a major source of income for many Caribbean nations, but also prevent fishermen from accessing their livelihood and could have disastrous effects on local coral reef and seagrass systems (Smetacek & Zingone 2013). Scientists are currently relying on local reports and testimony along with satellite images to track bloom magnitude and location. While the Gulf, Sargasso Sea, and Caribbean may experience the aforementioned stressors to varying degrees, the movement of *Sargassum* between them could negatively impact all three regions and beyond. Fortunately, Schell, Goodwin & Siuda (2015) report that the effects of the 2015 bloom were not felt in the Sargasso Sea however, as of yet, no such information concerning other regions, like the Gulf of Mexico, exist. In order to better understand differences/connections between these regions, a simultaneous survey of the Gulf of Mexico, Sargasso Sea, and outer Caribbean was performed.

Hypotheses

Given the importance of pelagic *Sargassum* to neuston biodiversity this study examined several factors believed to influence associated mobile faunal diversity, species richness, and community composition. Independent factors considered include *Sargassum* species and form morphology, aggregation pattern, and geographic region. (1) As a result of the proposed geographically distinct source regions of different pelagic *Sargassum* forms and their proposed pathways of dispersal via prevailing currents, mobile fauna diversity and community composition are expected to vary at different

geographic positions along proposed dispersal pathways. Accumulations of *S. fluitans III* and *S. natans VIII* are thought to disperse through the Gulf of Mexico to the Sargasso Sea and the NERR to the Caribbean, Gulf, and Sargasso Sea respectively, and are expected to accumulate species as they progress through the dispersal pattern. *S. natans I*, however, which remains in the Sargasso Sea, will have its highest diversity in its source region. Where it is found mixed with other species, its fauna diversity will likely be reduced. (2) Aggregation patterns (isolated clump, windrow, or mat) will have an effect on the abundance and diversity of fauna. Larger aggregations of *Sargassum* (rows and mats) will have higher abundance and diversity compared to isolated clumps because of the larger habitat surface area they offer. In addition, the colony condition, new growth, mature, and decline area, will likewise affect fauna abundance and diversity with healthier, optimal habitat supporting higher abundance and diversity. (3) *Sargassum* species and morphological differences will affect the types and diversity of associated mobile fauna. The compact, structurally diverse habitus of *S. fluitans III* will support a more diverse and abundant mobile fauna community than the more loosely compact *S. natans VIII* with *S. natans I* representing an intermediary between the two forms.

II. LITERATURE REVIEW

Early Descriptions of Sargassum

Sargassum was mentioned by Christopher Columbus in his September 20, 1492 journal entry. On this day, he describes his first sighting of the floating weed and the following day discovers "so much weed that the sea appeared to be covered with it" (Columbus, trans. Markham 1893). The name *Sargassum* is thought to be derived from the Portuguese word *salgazo*, a type of grape, likely inspired by the small floats that allow the algae to maintain its floating pelagic life cycle (Dickinson 1894, Kurmmel 1892). The earliest scientific classification of pelagic *Sargassum* was described by Linnaeus in 1753 who classified what is now known as *S. natans* as *Fucus natans* (Linnaeus 1753). Seventy years later, this species was reclassified by Gaillon and given its currently accepted name (Gaillon 1828). *S. fluitans*, the remaining pelagic species, was formally described and classified in 1914 (Børgesen 1914). It was not until the turn of the 20th century that field studies of pelagic *Sargassum* distribution were conducted, primarily, in conjunction with studies of surface currents, in attempts to define the boundaries of the Sargasso Sea. Interest in the taxonomy and associated fauna of pelagic *Sargassum* came about as an artifact of these distribution studies. Long disputed between scientists was if the algae were truly pelagic. Anecdotal observations and Hentschel's (1914) published work describe lighter, seemingly newer sections of *Sargassum* plants with little epizoa coverage as evidence that the algae vegetatively grows in the Sargasso Sea. Winge (1923) stipulates that the weed could not possibly come from benthic,

coastal locations because pelagic specimens had never been found with sexual organs while such organs were frequently found on attached forms.

Winge (1923) also provides the first detailed examination and descriptions of morphological forms or "species", of *Sargassum*. In describing the eight "species" or forms of the algae, Winge (1923) does not distinguish between *S. natans* and *S. fluitans* but rather numbers the types I-VIII. Types I-III, he characterizes as permanent flora of the Sargasso Sea or those that are most commonly found. Types IV-VIII were rarer and only found in western regions. Distinctions were made based on morphological differences including variation in blade length, width, and serration, bladder size, presence of thorns on stems, presence of spikes on the tips of bladders, bladder and blade density, branching frequency, and colony size. In 1939, Parr expanded on Winge's classification by identifying two further types and classifying them as either *S. natans* or *S. fluitans*; Parr describes *S. natans I, S. natans II, S. natans VIII,* and *S. natans IX* as well as *S. fluitans III* and *S. fluitans X*. Parr's study represented one of the first ever directed, large scale collections of *Sargassum*. Like Winge (1923), Parr (1939) identifies *S. natans I* and *S. fluitans III* as the most abundant species within the bounds of the Sargasso Sea but Parr's expanded collections also show *S. natans I* dominance in the Caribbean and Gulf of Mexico with *S. natans VIII* and *S. fluitans III* present but proportionally less common. Parr also summarizes arguments and provides evidence concerning the reproductive nature of *Sargassum*. He provides four lines of evidence towards the asexual budding hypothesis: (1) the algae must be able to withstand a drifting, pelagic existence for several years to explain its wide distribution, (2) ample

growth regions appear on specimens in the central Sargasso Sea, far from any coastal benthic locations, (3) simultaneous, region-wide frequency increases were observed during the summer and fall not merely at coastal boundaries, and, with Winge and Parr's advanced classifications which separated benthic from pelagic species (4) few benthic specimens were ever identified in the pelagic environment. On the rare occasion a fruiting specimen of *S. fluitans* was observed, it was found attached to the root of a mangrove leading Parr to postulate that one could induce sexual reproducation in pelagic *Sargassum* by attaching it to a substrate although acknowledging that this is an unlikely mechanism for pelagic *Sargassum* reproduction. It is primarily from these two sources on which modern studies and detailed identification of *Sargassum* species and forms are based.

Pelagic Sargassum

Genetic Studies

With its highly complex structure, pelagic *Sargassum* exhibits high intra-species morphological differences. While Winge (1923) and Parr (1939) managed to identify unique phenotypes, there is still uncertainty. Only very recently have genetic studies of *S. fluitans* and *S. natans* and their most common forms been undertaken. Thus far, species and form delineation has relied solely on the observation of morphological differences. Camacho et al (2015) conducted the first ever genetic examination of pelagic *Sargassum* included in their larger assessment of the genus. Through amplification of the nuclear Internal Transcribed Spacer 2 (ITS-2), chloroplast-encoded *rbc*S, and mitochondrial cytochrome c oxidase subunit 3 (*cox*3), regions used previously

in benthic *Sargassum* sequencing, they confirm a distinct lack of genetic diversity between the twenty-four unique species sequenced, also found by Mattio et al (2008), suggesting recent and rapid diversification. Sequencing of the brown algae cytochrome c oxidase subunit 1 (*cox*1) gene by the Sea Education Association (Olsen & Tonkin 2015) of three forms of pelagic *Sargassum*, *S. natans I, S. natans VIII*, and *S. fluitans III* revealed slight genetic differences (one basepair) between the two species and none between the two forms of *S. natans*. Because of this lack of genetic diversity, the classification of *S. natans* and *S. fluitans* as unique species is based upon a morphological foundation rather than a genetic one.

Sargassum Reproduction & Growth

Pelagic *Sargassum*, unlike benthic species, propagates through asexual reproduction. Termed thallus fragmentation, declining areas of *Sargassum* colonies are broken off of healthier portions and, due to their lack of viable bladders, sink (Kilar, Hanisak, & Yoshida 1992). When colonies are split, growth continues on both segments, forming fully mature individuals. Assuming all pelagic *Sargassum* undergoes this process, individuals of each species should be genetically similar although no large scale, within-species sequencing has been conducted to confirm this. While nearly one hundred years of pelagic *Sargassum* collections support the idea of asexual reproduction for floating plants, there have been a few exceptions. In addition to the aforementioned discovery of reproductive structures on attached *S. fluitans*, Moreira & Suarez (2002) reported the discovery of fertile structures on two specimens of *S. natans* and *S. fluitans* collected off Cuba. However, because these samples were collected in a coastal region, it

is possible that they are either misidentified benthic specimens or a rare occurrence of the type Parr (1939) observed.

Despite its potentially minimal genetic diversity, pelagic *Sargassum* is found throughout the Caribbean, Gulf of Mexico, the Gulf Stream, and Sargasso Sea. Its abundance varies both regionally and inter-annually (Deacon 1942, Parr 1939, Winge 1923). Unlike ephemeral floating algae, which persist longer at lower temperatures (Vandendriessche, Vincx, & Degraer 2007), *Sargassum* appears to be ideally adapted to its pelagic existence. It experiences its highest growth rates at higher temperatures and cannot survive in waters less than 18°C (Parr 1939, Winge 1923). These high temperatures also likely contribute to pelagic *Sargassum*'s fast growth rate which, over a two week period, has been observed to increase in weight by 47% and length by 20% (Howard & Menzies 1969). Laboratory studies by Hanisak & Samuel (1987) revealed species specific differences in preferred temperature range and growth rates. *S. fluitans* had a higher growth rate and fared better in a narrower, higher range of temperatures (24-30°C) than *S. natans*, which had a broader range (18-30°C). Both species halted growth below 12°C and above 30°C. Both *in situ* (LaPointe 1986) and laboratory experiments (Hanisak & Samuel 1987) revealed pelagic *Sargassum* to have a much faster growth rate than previously thought possible (Mann *et al* 1980, Michanek 1975). To protect itself from herbivory, *Sargassum* synthesizes polyphenolic toxins (Sieburth & Jensen 1969). Because it offers not only a physical habitat but a source of nutrients to a diverse faunal community, any dramatic loss of pelagic *Sargassum* is significant. Hanson (1977) found that *Sargassum* and its associated epiphytes (flora and fauna)

released a significant amount of dissolved organic carbon (DOC) in surrounding waters as well as making fixed nitrogen available to the community. While, even in the oligotrophic Sargasso Sea, these values were not significantly higher than plankton, the concentrated nature of pelagic *Sargassum* means that it supplies surface communities with a substantial quantity of fixed nitrogen.

Ecosystem Services

Sargassum not only benefits pelagic communities; even washed ashore, the algae provides significant benefits to coastal communities as well. It is well established that wrack, marine algae beach deposits, absorb wave energy and trap sediments although only one study has specifically examined *Sargassum* wrack. In a study of Galveston, TX beach erosion, Webster et al. (SEAS, unpublished report) observed significant seasonal accretion associated with peak *Sargassum* casting but no significant changes over the course of the year. They postulate that this lack of build-up, unlike most natural systems, is the result of frequent raking of marine detritus on Galveston beaches. In addition to erosion prevention, pelagic *Sargassum* depositions provide nutrient subsidies to dune plants, which also prevent erosion. Williams & Feagin's (2010) greenhouse based study of *Sargassum* addition resulted in growth enhancement of *Panicum amarum* (bitter panicgrass). In addition to the ecosystem services the beached algae provides, *Sargassum* in the open ocean that has lost flotation, provides a significant nutrient input to deep benthic communities. Compared to typical marine snow, pelagic *Sargassum*'s large "particle" size increases the likelihood of it sinking rapidly to the seafloor without a significant loss of biomass. Schoener & Rowe (1970) reported observing whole

Sargassum plants at depths >5,000m being consumed by brittle stars. Pelagic *Sargassum* may be a responsible for a significant portion of the vertical transport of organic material in addition to horizontal transport. In the ocean, on the seafloor, and on shore, pelagic *Sargassum* provides vital ecosystem services (South Atlantic Fishery Management Council 2002).

Sargassum *Distribution & Patterns*

Throughout its range, pelagic *Sargassum* is distributed by established surface currents. Waters in the North Equatorial Recirculation Region split and move either west and north of the Lesser Antilles or east, into the Caribbean Sea from which they enter the Gulf Loop Current. At the Florida Straits, these two currents reconnect and move into the Gulf Stream and eventually into the Sargasso Sea (Figure 4). After long periods of circulation, waters in the lower, eastward moving portion of the Sargasso Sea gyre can reenter the Caribbean (Frazier et al. 2014, Nowlin 1971).

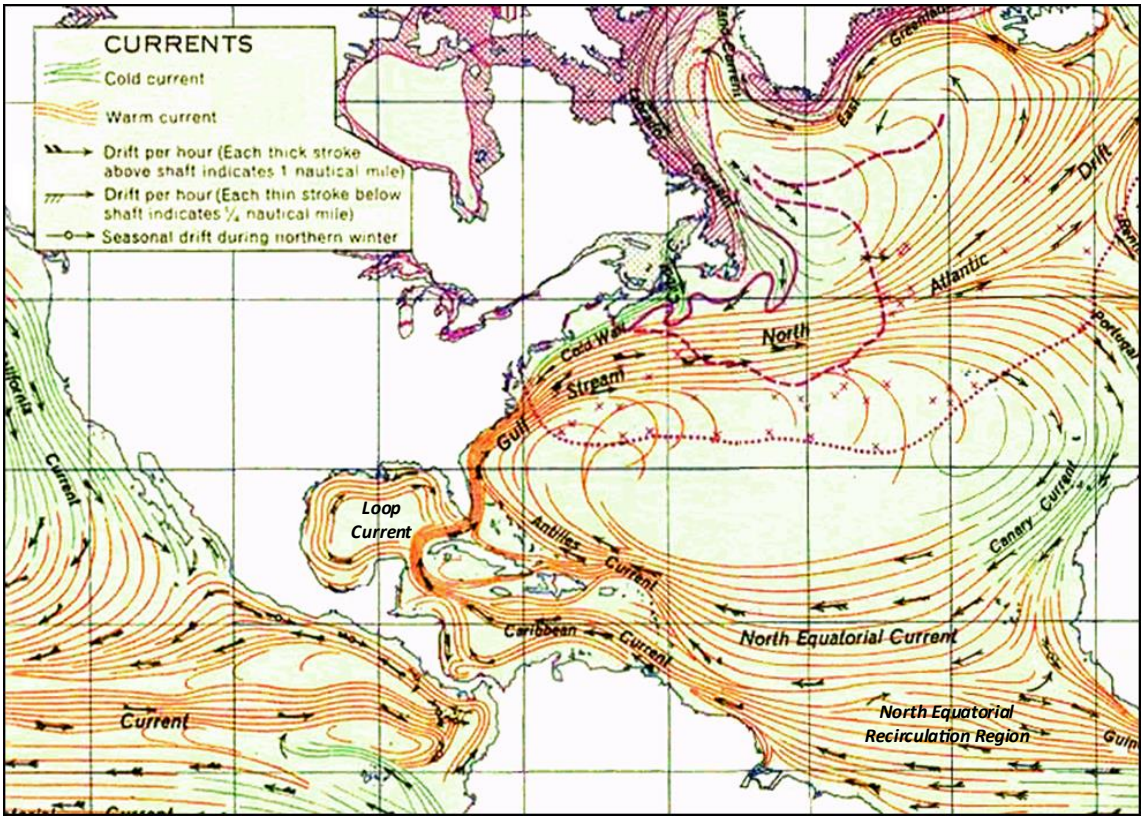

Figure 4: Map of north Atlantic currents including those that are known and hypothesized to transport *Sargassum* throughout its entire range. (United States Army Service Forces 1943).

Satellite imaging has allowed scientists to continuously track pelagic *Sargassum* distribution much more easily and efficiently than shipboard observations have provided but only for large accumulations of the algae. Resolution size limits the extent to which pelagic *Sargassum* can be detected in less dense aggregation patterns. The first detection of pelagic *Sargassum* by satellite was described by Gower et al. (2006) using the Maximum Chlorophyll Index (MCI) of the Medium Resolution Imaging Spectrometer (MERIS). Gower & King (2011) were able to track pelagic *Sargassum* aggregations on a

much larger scale albeit with 1200m resolution through the use of offshore imagery. They observed pelagic *Sargassum* moving from the Gulf of Mexico in the spring and early summer, into the Sargasso Sea during the fall and early winter, and, at the conclusion of their study, moving just north of The Bahamas. While this use of satellite technology has its advantages, its resolution compared to typical algae aggregation size likely prevents detection in many regions of pelagic *Sargassum*'s range. Large, easily detectable mats more commonly form in areas of slowly circulating water, like those found in central gyre locations, whereas fast moving currents are likely to break up these large aggregations, rendering the pelagic *Sargassum* undetectable to satellites. Thus, the use of satellites, in conjunction with field observations, is necessary to gain an accurate understand of *Sargassum* distribution and movement patterns.

The large mats observed first by Columbus and now via satellite are one of three aggregation patterns in which *Sargassum* can be found. In addition to mats, the algae can present as randomly distributed, isolated clumps or in long rows. These rows are the result of Langmuir circulation during which surface material aggregates at the intersection of the downwardly rotating sides of vortices running parallel to the ocean surface (Langmuir 1938). The spacing of these vortices and, therefore, collections of *Sargassum*, depends on wind speed with higher wind speeds associated with wider spacing (Faller & Woodcock 1964). While this formation develops at a minimum of $3ms^{-1}$, at some cutoff of high wind and waves, the pattern disintegrates leaving scattered, isolated clumps (Barstow 1983). Even without floating substrate, surface slicks as a result of Langmuir circulation have been found to concentrate both small fish and

zooplankton (Kingsford & Choat 1986). In windrows, when floating macroalgae begins to decay or is overgrown by epibionts, it can be forced downward in the water column (Barstow 1983). In the case of pelagic *Sargassum*, if it is forced below the critical depth of 100m, its floats will pop, the plant will lose buoyancy, and it will sink (Johnson & Richardson 1977).

Rafting Communities

While *S. natans* and *S. fluitans* form the only holopelagic biotic floating substrate, it is by no means the only source of drifting habitat. In their substantial summary of marine rafting ecology, Theil & Gutow (2005a, 2005b) categorize floating items into biotic and abiotic origins. Biotic substrates, which have a wide range of sizes, include macroalgae, like *Sargassum*, wood, seeds, other land-based plants, and animal remains. Abiotic substrates, which are typically less than 10cm in diameter, include natural volcanic pumice and anthropogenic litter (plastic, wood, and metal) and tar lumps. Apart from their size and composition, floating material also differs in the length of time it spends at the sea surface with abiotic material achieving higher longevity compared to biotic material. While they remain floating for lengthy periods of time, unless epibionts settle on abiotic substrates, they offer very limited nutrient resources for rafting fauna. The distribution of each material in surface waters is dependent on its source of origin. For example, anthropogenic material is found near regions of large human populations, macroalgae is more typically found in mid-latitudes, while floating seeds are more concentrated in the tropics. Because of the varying mechanisms by which

floating debris enters the ocean, most forms, in particular, macroalgae, experience high interannual variability (Kingsford 1992, ZoBell 1971).

For those types of floating material that can support fauna, the abundance and diversity of said fauna varies with an assortment of substrate characteristics including size, structural complexity, distance from shore, point of origin, and quality/age as well as oceanographic parameters like water temperature. The impact of macroalgae assemblage size on species richness, diversity, and overall abundance is highly variable in the literature. Given Huffaker's (1958) classic study on the impact of structural diversity on species diversity, one would predict that floating macroalgae with a complex three dimensional structure would support more species. While Vandendriessche et al (2006) found highest diversity on the less structurally complex *Fucus*, Gutow et al (2015) found that the more complex benthic *Sargassum* supported higher diversity. Clarkin et al (2012), meanwhile, found no significant difference between similarly structurally diverse macroalgae rafts and instead concluded that temperature was the cause of species differences. With respect to the influence of raft size on species richness and diversity, the general consensus is that larger raft volume/surface area weakly supports higher numbers of individuals (Fine 1970, Goldstein, Carson, & Eriksen 2014, Gutow et al 2015, Vandendriessche et al 2006), however, Clarkin et al (2012) reported no relationship.

Sargassum *Macrofauna – Close Associates*

The *Sargassum* Community

Of the many ecosystem services *Sargassum* offers, it can be argued that none are more important than the structural habitat it provides that supports an incredibly diverse pelagic community. The macrofauna that *Sargassum* supports can be broken down into four functional groups: (1) mobile epifauna, (2) sessile epifauna, (3) clinging fauna, and (4) associated nektonic fauna (Ekman 1967, Friedrich 1969). Mobile epifauna include groups like polychaete worms, snails, flatworms, and nudibranchs, which require a substrate on which they can move around. Sessile epifauna, on the other hand, which include hydroids, bryozoans, and tubeworms, remain permanently attached to a particular location on the substrate. Clinging fauna, like shrimp, crabs, seahorses, and frogfish, are typically found gripping to pelagic *Sargassum* but have limited ability to move between free-floating colonies. Adams (1960) divided the fourth category of associated nektonic fauna into random and deliberate species. Randomly associated species, typically self-buoyant pleustonic invertebrates like siphonophores, are often found tangled in pelagic *Sargassum* patches as currents and eddies concentrate floating surface material. Deliberately associated species, including free-swimming fish, sea turtles, and sea birds, are species that actively seek out pelagic *Sargassum* at some stage but that are not specifically adapted to a rafting regime. These species seek out the floating algae as a place to lay eggs, as protection for juvenile fish, as a resting place for sea birds and turtles, and as a source of food. Unlike ephemerally associated species, species that spend their entire lives hidden in pelagic *Sargassum* do so through the use of

camouflage, where an organisms blends in to a mosaic of environmental patterns, and plant-part mimicry, where an animal mimics the size and shape of a particular part of its habitat. Most associated species mimic the golden-brown color of their habitat. Hacker & Madin (1991) examined the coloration, size, and morphologies of two common species of shrimp, *Latreutes fucorum* and *Hippolyte coerulescens*. Along with significant intraspecies color variation, they found that the more slender *L. fucorum* closely associated with the fronds it so closely resembled while the more bulbous *H. coerulescens* was found closer to the main stalk, near collections of floats it mimics. They also found evidence of an ontogenetic shift from solidly colored juvenile individuals using plant-part mimicry, to larger, mottled adults, relying more heavily on camouflage.

Most studies examining pelagic *Sargassum* and its associated fauna have done so on a broad scale through observational analysis of differences between regions and substrate species and over time. Even before strong distinctions between pelagic *Sargassum* species and forms were made, scientific data concerning the algae's diverse community were being collected. Hentschel (1922) collected extensive observations on sessile epibionts. While these organisms obtained the majority of their food resources from pelagic sources, primarily micro-plankton, their small size indicated that the community was food limited as a result of the oligotrophic conditions within the Sargasso Sea. For bryozoans and hydrozoans, in particular, there was intense competition for space. Rapid colonization of new growth areas of pelagic *Sargassum* was possible in these two groups through extensive use of asexual reproduction.

Hydroids and bryozoans make up just two of the sixteen total groups of organisms comprised of 99 closely associated pelagic *Sargassum* species found in the Sargasso Sea, compiled into a key by Morris & Mogelberg (1973); a collection which does not include associated fish. Coston-Clements et al (1991)'s expanded list of species in the Gulf of Mexico and North Atlantic comprises 147 species of sessile and mobile fauna representing nine phyla and twenty three orders, and 111 species of fish associated with pelagic *Sargassum* at some point in their life representing thirty eight families. Of these species, a majority appears to be generalist omnivores and carnivores and none are known to be strict herbivores. Rafting omnivores typically consume detritus and plankton while carnivore species, like shrimp, crabs, and fish, consume smaller crustaceans and, in the instance of the *Sargassum* frogfish, *Histrio histrio*, smaller conspecifics. Associated fish consume rafting species as well as other, smaller fish species (Butler et al 1983).

Community Variation over Time

Fine's (1970) study of faunal variation over time in the Gulf Stream and Sargasso Sea is one of only a few species to identify pelagic *Sargassum* at the form level rather than just the species level. Although the author did not make distinctions of fauna association between their substrate (*Sargassum*) species and/or form, an attempt was made to distinguish differences over the course of a year. On pelagic *Sargassum* comprised of 99% *S. natans I* and *S. fluitans III*, Fine found large variation in fauna species diversity both between individual colonies and within seasons which prevented significant differences between seasons from being detected. While diversity shifts were

undetectable, significantly higher abundances were observed in the spring compared to fall samples. The author remarks that seasonal changes were likely not detected because this study was conducted over a relatively small area with both time and space as variables, and suggests a simultaneous survey over a large area with repeated sampling. Butler et al's (1983) larger study surveyed fauna near Bermuda, in the western North Atlantic, and Northern Caribbean. The authors observed dramatic changes in multiple species over the course of a year which they attributed not to oceanographic parameters directly but to *Sargassum* growth patterns which fluctuated with changes in sea surface temperature. During the spring, when temperatures rose and pelagic *Sargassum* was actively growing, communities tended to be simple, building in diversity as the colonies reached maturity and now contained a range of growth zones. Huffard et al (2014) used historical samples from 1966-74 and present-day collected during 2011-12 to compare community diversity changes across both small and large timescales. Between seasons, the authors observed a decrease in diversity, evenness, and abundance from summer 2011 through winter 2012. Over large time scales, they hypothesized a latitudinal shift in community diversity associated with increasing SST in the Sargasso Sea; however, from their limited data, no shift was evident. Overall, studies of temporal variation in pelagic *Sargassum* communities reveal significant shifts over the course of a year typically masked by high interannual variability.

Regional Differences

Thus far, studies of geographical variation in pelagic *Sargassum* communities have primarily been limited to comparisons within the Sargasso Sea and nearby Gulf

Stream. Early on, Timmerman (1932) observed higher values of species diversity in the northern Sargasso Sea (including the Gulf Stream) compared to southern areas closer to the Caribbean. Stoner & Greening's (1984) examination of *Sargassum* in the Gulf Stream and Sargasso Sea revealed high intra-regional similarity with in the Gulf Stream, low intra-regional similarity in the Sargasso Sea, and low inter-regional similarity. Sargasso Sea samples were more evenly distributed with the most dominant species, *Litiopa melanostoma*, comprising only 25% of the total fauna on average. Gulf Stream *Sargassum*, on the other hand, was significantly dominated by *L. fucorum* with a mean proportion of 70%. With respect to food web analysis, using trophic levels designated by Butler et al (1983), the authors observed a higher proportion of large, high trophic level omnivores in Gulf Stream samples while Sargasso Sea samples contained more small omnivores feeding on larger proportions of low trophic level, sessile epibionts. Keller (1987) also analyzed Gulf Stream and Sargasso Sea waters across a longitudinal gradient although at a comparatively smaller scale. The author concluded that significant decreases in epifauna diversity were linked with similarly decreasing nutrient concentrations in surrounding waters. A larger study conducted by Niermann (1986) in the southern Sargasso Sea, used neuston tows and aggregate collections of pelagic *Sargassum* at 207 stations. While this collection method did not allow the authors to distinguish faunal association between *Sargassum* species/form, they did identify proportions of each form found with *S. natans I* comprising 80-90% of all stations, followed by *S. fluitans III* (15-23%), and other morphologically rare forms (*S. natans II* and *Sargassum V*, 2-5%). The authors found an appreciable difference in abundance of

the hydroid, *Membrainipora*, which was higher in the northern Sargasso Sea, but not in the abundance of the hydroid *Clytia*. Conversely, Sehein et al (2014) observed distinct genetic populations of the *Sargassum* shrimp, *L. fucorum* although no regional pattern of distribution was observed.

Association with *Sargassum* Species

Along with regional and temporal comparisons, a few studies have made comparisons in faunal association with substrate species. In addition to his descriptions of *Sargassum* forms, Winge (1923) noted that *S. fluitans III* was nearly always overgrown with the hydroid, *Aglaophenia latecarinata*, while *S. natans II* had only one occurrence. Hentschel (1921) marked similar differences in epizoa between broad and narrow-bladed pelagic *Sargassum* (species/forms not described). Weis (1968) conducted a small study in Gulf Stream waters consisting of two *S. natans* and two *S. fluitans* samples. Although form distinctions were not made, based on typical abundance estimates and descriptions of the fronds of *S. natans* as narrower than *S. fluitans*, the species represented here were likely *S. fluitans III* and *S. natans I*. *S. natans* was found to have fewer species and lower diversity than *S. fluitans* which the author postulates is due to the overall lower available surface area of *S. natans* because of its smaller fronds. In addition to their regional comparisons, Stoner & Greening (1984) also made comparisons of diversity across pelagic *Sargassum* species. Of the 23 total fauna species found, 21 were found on *S. fluitans* and 22 on *S. natans*. The authors concluded that substrate species had little influence on community assemblages; only one species, *L. melanostoma*, was more abundant on one species (*S. natans*, 20.2%) versus the other (*S.*

fluitans, 3.3%). Calder (1995) conducted a study in the waters around Bermuda to test for differences in hydroid association with pelagic *Sargassum* species. Seven of the ten most common species reported in the literature were found with the highest number of unique species found on *S. fluitans*. *S. natans* was dominated by a single species, (average frequency of 83%) while *S. fluitans* had a more diverse array of abundant species (average frequency of 22-37%). Thus far, few studies have identified *Sargassum* species or form and the studies that have done so have more frequently examined differences in sessile epibionts only.

Sargassum *Macrofauna – Loose Associates*

Icthyofauna

Recently, the majority of pelagic *Sargassum*-associated fauna studies have been those concerning deliberately associated nektonic fauna like fish. Dooley (1972) used purse seine and dip net samples to collect weed within a given area and associated fish off in east Florida coastal waters. The author divided 54 species into four categories of association pattern: closely associated, moderately associated, coincidentally occurring, and seasonally occurring. Within closely associated species, the most abundant fish were *Stephanolepis hispidus* and *H. histrio*, although these numbers varied seasonally. Given the species, age classes, and location of more frequently occurring fish, Dooley concludes that these organisms rely on pelagic *Sargassum* primarily for food and shelter. Overall more fish biomass was found to be correlated with peak weed biomass during the spring and summer. Bortone et al (1977) collected associated fish in the eastern Gulf of Mexico using primarily dip nets and occasionally, neuston tows. This was the first

study to remark on the possibility of a sampling bias when using smaller dip nets to sample fish, larger individuals of which, are able to dive beneath the reach of the net. In the eastern Gulf of Mexico, stations were dominated by *S. hispidus* (reported genus: *Monocanthus*) while, unlike Dooley's (1972) frequencies, *H. histrio* was comparatively rare. In addition to regional differences, the authors also observed a significant increase in diversity moving from inshore to offshore waters. Overall, they postulated that Gulf pelagic *Sargassum* supported fewer species and was dominated by a single species because its community is less stable as a result of the circulation patterns that replenish *Sargassum*. While Florida Atlantic coastal waters are supplied by the generally geographically stable Gulf Stream, the Gulf of Mexico is supplied by the Caribbean and Loop Currents the latter of which displays high variability (Sturges & Evans 1983).

In a Master's thesis, Settle (1993) collected 104 fish species in the South Atlantic Bight region of the Western Atlantic. Unlike Bortone, Hastings, & Collard (1977), Settle found both decreasing diversity and abundance with increasing distance from shore. Diversity was highest in the spring and summer over the entire region while abundance decreased from fall through winter. For the majority of stations, abundance and total fish biomass were positively correlated with pelagic *Sargassum* biomass. Moser, Auster, & Bichy (1998) used ROV surveys in the Gulf Stream rather than traditional net sampling to avoid underrepresenting large juvenile and adult fish under pelagic *Sargassum* mats, dispersed clumps, and in open water. They also conducted dip net sampling in the same region for a comparison of methods. Of the 31 total species identified using the two methods, juveniles dominated dip net samples while more adults were spotted using the

ROV. Species abundance increased with increasing pelagic *Sargassum* aggregation size. Casazza & Ross (2008) also used combined net and video sampling to survey in Gulf Stream waters with pelagic *Sargassum* and in open waters. Net sampling revealed higher species richness, overall abundance, and overall fish size associated with large algae aggregations. The majority of fish in both habitats were juveniles, primarily *S. hispidus*. Video surveys revealed a layered structure with smaller fish remaining closer to pelagic *Sargassum* than larger individuals.

Like Bortone, Hastings, & Collard 1977, but unlike Setter (1993), Wells & Rooker (2004) also found a positive correlation between both abundance and diversity with distance offshore. Of the 36 species found using a purse seine net, 97% were comprised of seven species, and 95% were in early life stages leading the authors to conclude that Gulf *Sargassum* serves as a significant nursery habitat. Rooker et al (2006) performed a stable isotope analysis in the same region of the Gulf to determine the primary food source and trophic levels of members of the pelagic *Sargassum* community. Smaller, invertebrates occupied the lowest trophic levels, while juvenile fish were secondary heterotrophs, and adult fish were tertiary consumers. The primary source of organic matter to the community was determined to be particulate organic matter (POM) rather than the *Sargassum* itself. In the central north Gulf, Hoffmayer et al (2005) conducted a large, multiyear study of fish in and below pelagic *Sargassum* mats. Like Moser, Auster, & Bichy (1998), the authors observed significant layering of age classes with depth. Diversity was lowest within pelagic *Sargassum* itself although abundance was very high. Sub-surface tows had moderate diversity and low abundance

while areas directly adjacent to mats had the highest observed diversity. Overall, large pelagic *Sargassum* aggregations are magnets for high levels of fish diversity and abundance in often nutrient poor areas of the ocean.

Other Associates

Pelagic *Sargassum* is not exclusively utilized by deliberately associated nekton like fish; other marine species like turtles and seabirds utilize large rafts for protection, food, and areas of rest. In the South Atlantic Bight region of the Atlantic, Haney (1986) observed 30-40 times greater abundance of birds in areas with the algae compared to areas without. Seasonal variation in migratory species correlated with similar changes in pelagic *Sargassum* abundance. The author concluded that seabirds were attracted to the mats because their concentrated communities provide efficient foraging opportunities. Juvenile sea turtles also heavily rely on pelagic *Sargassum* aggregations. Carr (1987) performed the first large scale survey of sea turtle presence in *Sargassum* throughout the entirety of its distribution. Through direct sampling and indirect accounts, the author showed how juvenile turtles were able to find a reliable supply of food during their "lost years." Witherington, Hirama, & Hardy (2012) performed a more focused study examining age classes, daily use of pelagic *Sargassum*, and stomach content analysis. Both post-hatchlings and juveniles were observed to spend 97% of the daytime and 87% of the nighttime within 1m of the surface and near pelagic *Sargassum*. A majority of their food was composed of *Sargassum* macrofauna, but marine plants (i.e. *Sargassum*) and plastics also made up a significant portion. Adults also use pelagic *Sargassum* mats as cleaning stations where crabs remove epibionts on the turtles' shells that cause drag

(Frick, Williams, & Veljacic 2000). Mansfield et al's (2014) satellite tracking of neonate turtles revealed that, in addition to foraging and protection benefits, pelagic *Sargassum* also provides an ideal thermal habitat. Larger aggregations of the algae prevented surface water circulation, which, along with pelagic *Sargassum*'s composition and coloration, resulted in higher SST's compared to surrounding waters without weed. The authors concluded that even a small temperature increase could result in a boost to metabolic rates in a small bodied, exotherm. While seabirds and sea turtles may not spend the entirety of their lives amongst *Sargassum*, the temporary benefits it provides them are significant.

Threats to Sargassum *Communities & Conservation*

Conservation Measures

While scientist have been aware of the importance of pelagic *Sargassum* and its associated community for quite some time, recognition of and attempts to protect this uniquely vital ecosystem are a quite recent development. After private companies began, unregulated *Sargassum* harvesting, the United States' South Atlantic Fishery Management Council implemented the Fishery Management Plant for Pelagic *Sargassum* Habitat in the South Atlantic Region in 2003 which created strict restrictions on commercial harvesting (SAFMC, 2002). *Sargassum* was designated as an essential fish habitat for commercially important species as well as a protected habitat for juvenile turtles. Harvest, using allowed methods, was restricted to less than 5,000 pounds per year, collected from offshore regions during certain times of the year. A larger, international effort to protect the Sargasso Sea, including the *Sargassum* community,

was initiated by the Sargasso Sea Alliance (SSA) in 2010 which was a multinational collection of scientists, international marine conservation groups, and private citizens interested in preserving the unique region (Laffoley et al 2011). Founded by the Government of Bermuda, centrally located in the Sargasso Sea, the SSA aimed to gain support from international organizations and governments bordering the Sargasso Sea to motivate legal protection for the area. In 2014, with the signing of the Hamilton Declaration, the governments of The Azores, Bermuda, Monaco, the UK, and the USA committed to a non-binding collaboration towards the conservation of the Sargasso Sea outside the Exclusive Economic Zone (EEZ) and Territorial Sea of Bermuda. The SSA has since become the Sargasso Sea Commission which fulfills a stewardship role connecting the aforementioned governments with other interested and informed parties.

Marine Pollutants

While not intimately associated, the co-occurrence of pelagic *Sargassum* and petroleum products can have disastrous implications for the community. Like *Sargassum*, tar lumps are buoyant and moved across the ocean surface by winds and surface currents and, therefore, accumulate in areas of downwelling, like windrows (Butler et al 1983). While its association with pelagic *Sargassum* is irregular, tar lumps have been found to stick to the algae, increasing the time period over which contamination can occur (Butler 1975). Morris et al (1976) conducted a study to determine the extent to which petroleum and biogenic hydrocarbons were transferred in the *Sargassum* community and found that hydrocarbons did not increase in successive trophic levels. While not passed up the food chain, accumulation of hydrocarbons in

Pelagic *Sargassum* and members community is still significant and has toxic effects (Burns & Teal 1973). At the organismal level, high hydrocarbon concentrations can lead to impairment of feeding and reproduction and increased susceptibility to disease (Capuzzo 1987). These effects are felt most strongly during early developmental stages which, in a nursery habitat like a *Sargassum* mat, could have negative population-level impacts. Johnson & Braman's (1975) study of heavy metals, which are trophically concentrated, in the *Sargassum* community found that barnacles and shrimp disproportionately accumulated higher concentrations of germanium and mercury that other organisms, whose levels reflected those of the surrounding seawater. Marine pollutants not only affect organisms directly but can also affect the algae itself. Thanks in large part to stricter international regulations concerning oil tank cargo cleaning, tar presence, at least in the Sargasso Sea, has decreased over the last twenty years (Peters & Siuda 2014). In locations where the drilling industries effects are felt more strongly, however, the effect of floating hydrocarbons has far from decreased. Powers et al (2013) studied the impacts of the Deepwater Horizon oil spill and subsequent cleanup efforts on the differential buoyancy lifetimes of *S. natans* and *S. fluitans*. Their study, consisting of four trials of a control, oil, dispersant, and oil and dispersant, revealed that the presence of oil, with or without dispersant, negatively impacted the proportion of pelagic *Sargassum* at the surface. This effect was more pronounced in *S. natans*, which sank completely after only 48 hours, compared to *S. fluitans* which was more likely to remain at the surface. For communities associated with a particular species of *Sargassum*, the impacts of an oil spill, while already disastrous, could have disproportionate impacts.

Atypical Blooms

The most current and pressing issue concerning pelagic *Sargassum* is the atypical occurrence of massive blooms in the Caribbean and Gulf regions. First observed in 2011, a bloom 200-fold higher than the eight year average dispersed throughout the southern Caribbean and across the Atlantic, reaching as far as Sierra Leone and Ghana. Satellite imagery suggested that the unusual bloom was sourced from much further south than usual, in the North Equatorial Recirculation Region, where conditions were conducive to growth and consolidation (NERR) (Gower, Young, & King 2013, Johnson et al 2012). Massive accumulations near and onshore affected Caribbean tourism and caused food shortages in Western Africa where aggregations, extending for miles offshore, tangled fishing nets and prevented small boat movements (Smetacek & Zingone 2013). In the northwestern Gulf of Mexico, Texas A&M University at Galveston created the *Sargassum* Early Advisory System (SEAS) using LANDSAT satellites to track blooms nearing shore in an attempt to forewarn and prepare beach management efforts (Webster & Linton 2013). Not only is this important for the tourism industry, knowledge of future events is also vital for endangered Kemp's Ridley sea turtles (*Lepidochelys kempii*), large populations of which, return to nearby beaches every year to nest. Turtles caught up in *Sargassum* piling up on shore were buried or crushed by heavy equipment used to remove the algae (Rice 2014). For those individuals that are able to avoid human removal efforts, dense layers of the seaweed can prevent access the sand in which eggs must be laid. For those nests that manage to get laid, few ever hatch before they are destroyed by bulldozers or by the anoxic conditions produced by nearly a meter of

decaying *Sargassum*. If young turtles do manage to hatch successfully, their progress out to sea is often hindered by thick layers of the weed preventing turtles from using waves to navigate or even from surfacing (Maurer, De Neef, & Stapleton 2015).

Recently, two blooms have occurred. One localized but large bloom occurred off the coast of Galveston, TX in the summer of 2014. In one day, a three mile stretch of beach had a record 8,400 tons wash ashore in a 24 hour period. In 2015, another large scale bloom occurred throughout the southern Caribbean. Few scientists have conduced field studies in the region but local newspapers reported inundation events larger than ever before. As of yet, no one has been able to connect these blooms with a specific cause. In addition to the blooms, 2015 also marked a shift in pelagic *Sargassum* species distribution. In surveys in the Caribbean and Sargasso Sea, Schell, Goodwin, & Siuda (2015) reported that a typically rare form of *Sargassum*, *S. natans VIII* was suddenly very abundant, again, for, as yet, no explainable reason. These ocean-scale blooms have the potential to dramatically affect not only associated fauna but human lives and industries as well.

III. METHODS

Sargassum *Collection and Processing*

Samples were collected during the spring and summer of 2015 from the northern Gulf of Mexico (April – July), eastern Caribbean (February – March), and the Sargasso Sea (April - May). Samples in the Caribbean and Sargasso Sea were collected by the Sea Education Association's C-257 and C-259 cruises respectively. Samples obtained from the Gulf of Mexico within the Flower Garden Banks National Marine Sanctuary were collected under National Marine Sanctuary Permit FGBNMS-2015-003. From each region a subset of samples were collected from multiple stations (Sargasso Sea: 11 stations, 87 samples, Caribbean: 10 stations, 32 samples, Gulf of Mexico: 14 stations, 128 samples) (Figure 5).

Here, a station was defined as a single location with a large mat, established windrow(s), or scattered free-floating clumps within 100m of each other. Multiple individual colonies were dip-netted at each station as replicates using a 333 µm mesh net with dimensions measuring 0.45 x 0.35 x 0.40 cm with an approximate opening of 0.15 m^2 and initially placed in individual 5-gallon buckets containing seawater. However, free-swimming pelagic fish in or near *Sargassum* and/or sea turtles in the floating weed were not collected during this study. Surface water temperature, salinity, time of day, and sea state were also recorded at each station.

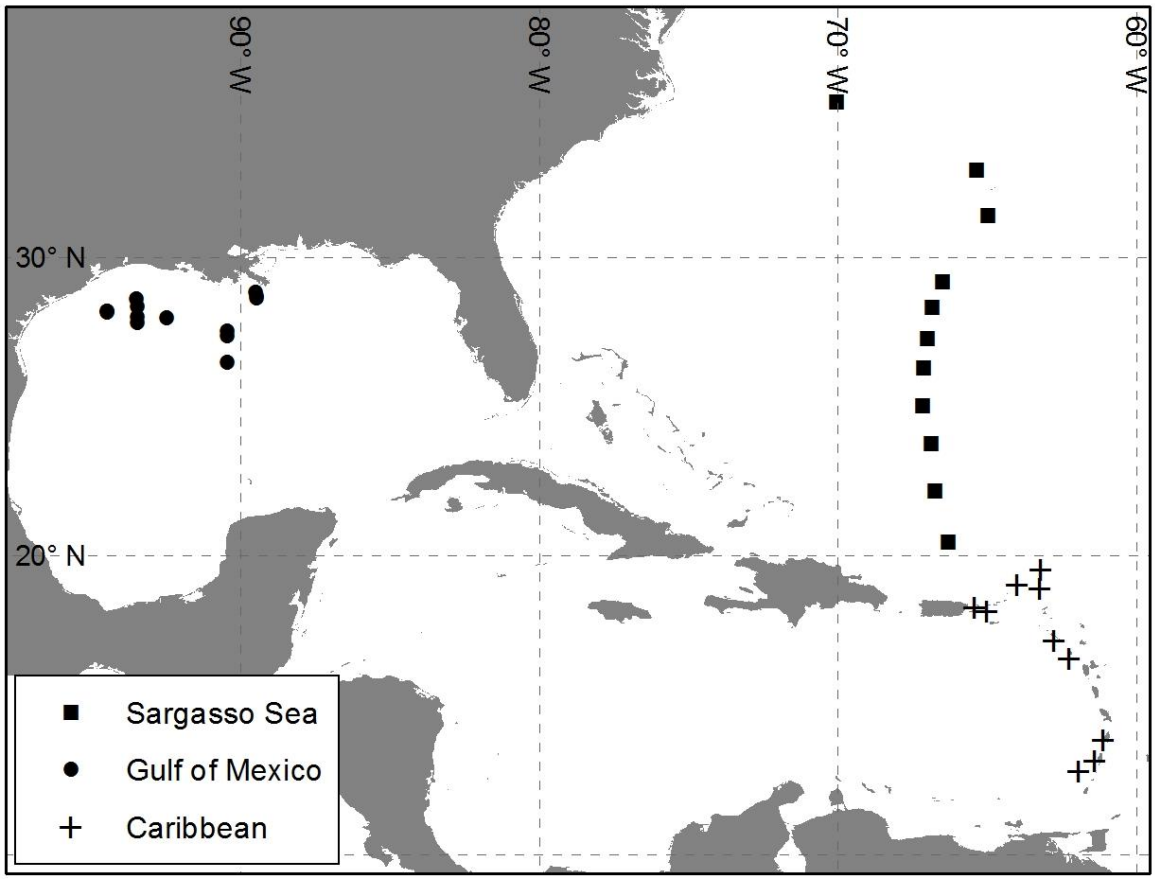

Figure 5: Map of station locations in the Gulf of Mexico (circle), Sargasso Sea (square), and Caribbean (cross) sampled during the spring/summer of 2015.

Only mobile fauna were collected as part of this study because of their importance as a food source in what is considered an essential fish habitat (Coston-Clements et al 1991, Witherington et al 2012). Mobile fauna collected with the *Sargassum* were carefully separated using a 333 µm mesh sieve and transferred to a 250 ml specimen jar with 70% ethanol for preservation and later analysis. To ensure an

accurate survey of fauna, colonies were meticulously examined (~15 minutes per sample) to remove those cryptically colored species which were not dislodged by flushing with seawater alone. Sessile fauna, including tubeworms and hydroids, were not analyzed as part of this study but percent coverage of each taxon was recorded. Wet weight of pelagic *Sargassum* was obtained using a spring scale and photographed against a 1 cm^2 grid pattern to determine approximate area. From these photographs colony condition was also determined. Colony condition was expressed as a percent of areas in stages of growth, succession, and decline which are determined through visual examination (Niermann 1986, Ryland 1974, Stoner & Greening 1984). A small clipping of each pelagic *Sargassum* colony was preserved along with mobile fauna for species and form identification.

Pelagic *Sargassum*-associated mobile fauna were identified to the lowest taxon using the Bermuda Biological Station's "Identification Manual to the Pelagic *Sargassum* Fauna" (Morris & Mogelberg 1973). Juvenile forms of unlisted fish species were identified with the assistance of Dr. R.J. David Wells (Texas A&M University at Galveston). *Sargassum* species and form were identified using Parr's (1939) and Winge's (1923) publications, although there have been no additional published reports on the formal botanical classification of what Parr and Winge called "forms" or "varieties" of *Sargassum*. While the terms form and variety have formal botanical definitions, in Parr's study and for the purposes of this study, the term form will be used to distinguish between morphologically unique classifications of pelagic *Sargassum*.

Data Analysis

Analyses were performed to examine differences in associated macrofauna species abundance, richness, evenness, and diversity within each of the three regions and between regions. The impact of *Sargassum* species and form differences, aggregation pattern, and colony size and condition on community diversity was also assessed. Oceanographic parameters including SST (sea surface temperature) and SSS (sea surface salinity) were compared across regions as potential explanatory predictors of pelagic *Sargassum* and associated fauna distribution. Analysis of covariance (ANCOVA) and the Wilcoxon Rank-Sum Test (for non-normally distributed data) were used to test for these differences. The Shannon-Weiner diversity index:

(1) $$H = -\Sigma[p_i * \ln(p_i)]$$

where p_i is the proportion of species i in the region, with outputs ranging from 0 to 1, was also calculated to compare between regions. This index was chosen because it gives more weight to rare species of which there were many. Species evenness:

(2) $$E = H / H_{max}$$

where H is the Shannon-Weiner index and H_{max} is the maximum possible diversity or the natural log of the total number of species was also calculated to determine the equitability of species abundances. Unique species to pelagic *Sargassum* aggregations and ocean regions were identified as well. Community composition differences between regions and pelagic *Sargassum* species were determined using contingency analyses and the Cochran-Mantel-Haenszel test (CMH). All statistics analyses were conducted using JMP® Pro 12.0.1 from SAS Institute Inc.

IV. RESULTS

Physical Setting & Sargassum *Frequency*

During the spring and summer of 2015, the Gulf of Mexico, Caribbean, and Sargasso Sea presented significantly different physical settings at the ocean's surface. Wilcoxon Rank-Sum Tests were used for the following non-normal data. All three regions had highly significant ($p<0.01$) differences in temperature with the Gulf as the warmest (mean = 29.1°C ± SD = 2.2), followed by the Caribbean (26.8°C ± 0.2), and the Sargasso Sea (24.8°C ± 2.0). Differences ($p<0.01$) were also found in surface salinity values, the Sargasso Sea with the highest salinity (36.6 ± 0.2), the Caribbean (36.1 ± 0.4), and the Gulf with the lowest values (33.7 ± 1.8), all highly significant. The highest winds were found in the Caribbean (15.3 kts ± 4.7), followed by the Sargasso Sea (10.6 kts ± 5.0), and the Gulf (8.4 kts ± 3.8) ($p<0.01$). Gulf surface waters were characterized by a relatively wide range of low salinities and a wide range of higher temperatures. The Sargasso Sea displayed a wide range of temperatures in the lower spectrum and a very narrow range of high salinity values. The Caribbean was very narrowly confined in salinity (high) and temperature (moderate) (Figure 6). Within the Sargasso Sea, a steady decrease in temperature with increasing latitude was observed beginning at 25°N (Figure 7).

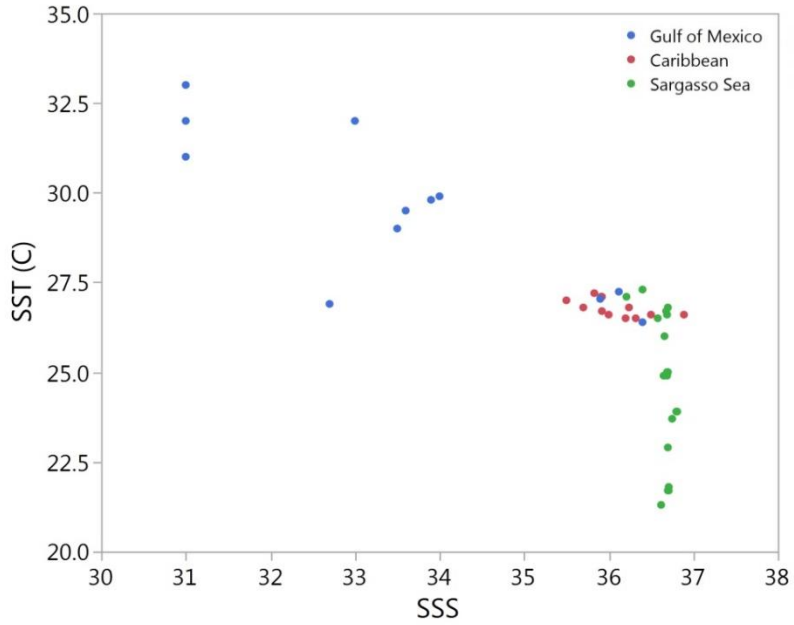

Figure 6: SSS and SST for the Gulf of Mexico, Caribbean, and Sargasso Sea.

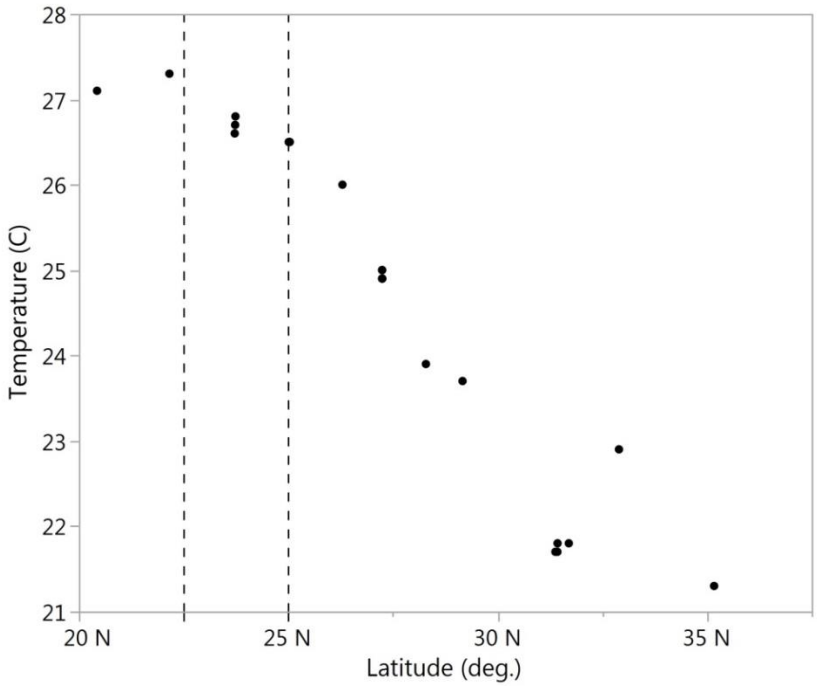

Figure 7: Decrease in temperature within the Sargasso Sea with increasing latitude was observed beginning at 25°N. Dashed lines mark 22.5°N, the northern boundary for *S. natans VIII*, and 25°N, the division between *S. fluitans III* to the south and *S. natans I* to the north.

A total of 13.2 kg of pelagic *Sargassum* was collected and processed as part of this study: 9.1 kg from the Gulf, 1.4 kg from the Caribbean, and 2.7 kg from the Sargasso Sea (Table 1).

Table 1: Mass (g) of pelagic *Sargassum* collected from the Caribbean, Gulf of Mexico, and Sargasso Sea.

Region	***S. fluitans III***	***S. natans I***	***S. natans VIII***	**Total**
Caribbean	572.0	16.0	792.5	1,380.5
Gulf of Mexico	5,545.0	0	3,560.0	9,105.0
Sargasso Sea	653.8	1,659.5	427.6	2,740.9
Total	6,770.8	1,675.5	4,780.1	13,226.4

Three pelagic species and forms of *Sargassum*, *S. fluitans III*, *S. natans I*, and *S. natans VIII*, were found in the three regions in significantly different ratios (CMH test, $p<0.01$). *S. fluitans III* and *S. natans VIII* were found in all three regions while the majority of observed *S. natans I* was restricted to the Sargasso Sea. While *S. fluitans III* and *S. natans VIII* were well mixed in the Gulf of Mexico and Caribbean, the three forms of pelagic *Sargassum* exhibited distinct geographic ranges in the Sargasso Sea. *S. natans VIII* was rarely found above 22.5°N while *S. natans I* was rarely found below 25°N. *S. fluitans III* was found intermixed with *S. natans VIII* and, to a lesser extent, *S. natans I* but generally remained constrained below 25°N (Figure 8).

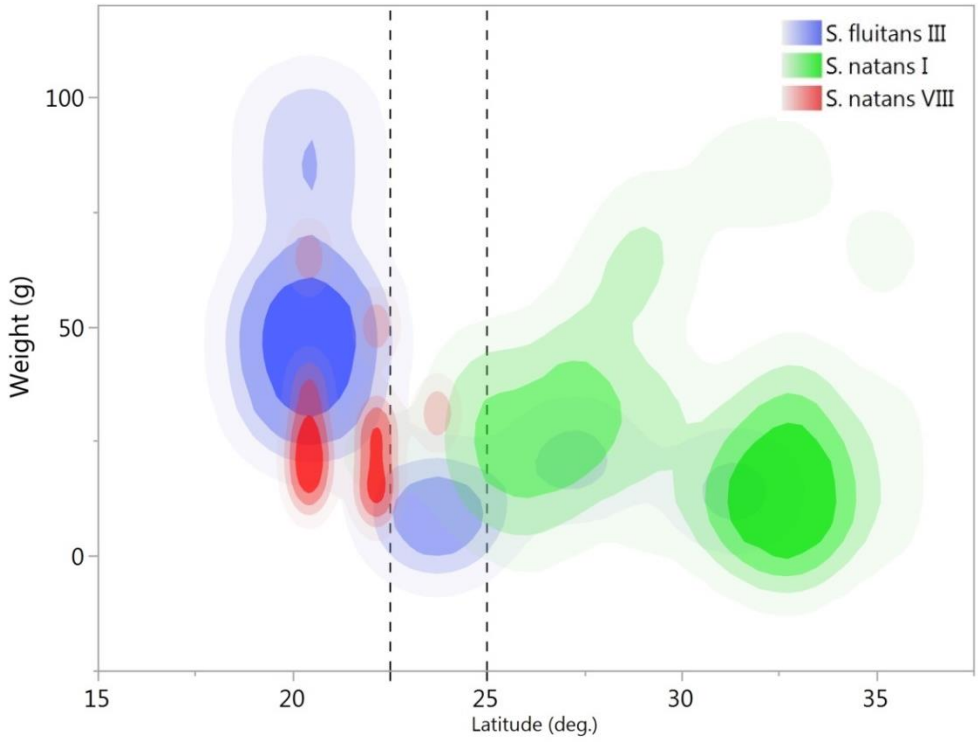

Figure 8: Latitudinal variation in *Sargassum* species weight distribution in the Sargasso Sea. *S. natans VIII* was rarely found north of 22.5°N while *S. natans I* was rarely found below 25°N. *S. fluitans III* was found intermixed with *S. natans VIII* but extended further, up to 25°N.

Regional Fauna Diversity by Pelagic Sargassum *Species*

The Sargasso Sea had the overall greatest diversity (H=1.15), followed by the Caribbean (0.91), and the Gulf of Mexico (0.74). A similar trend is present for multiple measures of diversity as well as evenness and effective number of species (Table 2).

Table 2: Comparison of regional differences in effective number of species, diversity (Shannon-Weiner), and evenness.

		Caribbean	Gulf of Mexico	Sargasso Sea
Effective no. of spp.	e^H	2.48	1.20	3.16
Shannon-Wiener Index	H	0.91	0.74	1.15
Evenness	E	0.37	0.07	0.64

Measures of fauna diversity and evenness for pelagic *Sargassum* forms within each region reveal different trends (Table 3). *S. fluitans III* has its lowest species diversity and evenness in the Gulf (H=0.74, E=0.27) and is higher in the Sargasso Sea (H=0.94, E=0.38), closely followed by the Caribbean (H=0.96, E=0.53). *S. natans I* in the Sargasso Sea had the highest diversity measurement of all *Sargassum* species and regions (H=1.22) and was relatively even in its species abundances (E=0.49). Because only two samples of *S. natans I* were found in the Caribbean, diversity measurements were not calculated. *S. natans VIII* had its greatest species diversity and evenness in the Caribbean (H=0.74, E=0.41) and has nearly identical, lower diversity and evenness in the Gulf (H=0.61, E=0.22) and Sargasso Sea (H=0.62, E=0.25). Frequencies for

common fauna species (see Table 6) for *S. fluitans III* and *S. natans VIII* were significantly different between regions (CMH, $p<0.01$). While unique species for each region were noted, evenness had the largest impact on diversity results. Pelagic *Sargassum* colony condition (growth, succession, and decline) also varies significantly between regions for each species (Table 4).

Table 3: Evenness and species diversity (Shannon-Weiner) measurements for pelagic *Sargassum* forms within each region.

	S. fluitans III	***S. natans I***	*S. natans VIII*
Evenness (E)			
Caribbean	0.53		0.41
Gulf of Mexico	0.27		0.22
Sargasso Sea	0.38	0.49	0.25
Diversity (H)			
Caribbean	0.96		0.74
Gulf of Mexico	0.74		0.61
Sargasso Sea	0.94	1.22	0.62

Table 4: Colony condition (area of growth, succession, and decline) across regions for each pelagic *Sargassum* form. Different letters indicate significant differences between the regions (Wilcoxon Rank-Sum Test multiple pair comparisons).

		Gulf of Mexico	Caribbean	Sargasso Sea
S. fluitans III	% Growth	22.9 [a]	17.1 [a,b]	10.0 [b]
	% Succession	28.5 [a]	57.1 [b]	57.8 [b]
	% Decline	48.6 [a]	31.9 [b]	25.8 [b]
S. natans I	% Growth			14.2
	% Succession			55.3
	% Decline			30.2
S. natans VIII	% Growth	32.7 [a]	12.8 [b]	15.0 [b]
	% Succession	27.9 [a]	43.1 [b]	46.7 [b]
	% Decline	39.8 [a]	43.4 [a]	38.3 [a]

Effect of Aggregation Pattern & Regional Colony Differences

Rows were the most commonly sampled aggregation patterns (51.7%) compared to isolated clumps (48.31%). Only one large mat was sampled, in the Gulf of Mexico, and thus was not included in the analysis. Across all regions, rows were observed more frequently at higher wind speeds (12.7 kts) than dispersed clumps (8.7 kts) ($p<0.03$). Despite this finding and the significantly different wind speeds in each region, no difference in frequency of aggregation patterns was found between regions. Samples collected from rows did not support higher species richness or total fauna abundance than isolated clumps. However, samples collected from rows did have greater average masses and smaller areas of decline than isolated clumps (Gulf of Mexico and Sargasso Sea) (Table 5).

A weakly positive relationship was observed between average individual colony weight and the number of individuals (R^2 = 0.38, $p<0.01$). The Caribbean supported significantly ($p<0.01$) more individuals per gram of pelagic *Sargassum* (4.27) than the Gulf of Mexico (2.63) or Sargasso Sea (2.59) (Figure 9). Although colony weight did not differ significantly between pelagic *Sargassum* forms when controlled for within form differences between regions, there was a significant overall regional difference between the Gulf of Mexico (63.3g) and Caribbean (43.1g, $p=0.02$) and the Gulf of Mexico and the Sargasso Sea (33.4g, $p<0.01$). Colony condition also varied significantly between regions. The Gulf of Mexico had a greater extent of growth area (26.7%, $p<0.01$) compared to the Caribbean (15.2%) and Sargasso Sea (12.6%), which were similar. The Gulf of Mexico also had significantly more area in decline (45.7%, $p<0.01$) than either the Caribbean (33.8%) or Sargasso Sea (31.6%). Lastly, pelagic *Sargassum* in the Gulf of Mexico presented with the lowest area of successional growth region (27.6%) which was significantly different ($p<0.01$) from the Caribbean (51.0%) and Sargasso Sea (55.6%) (Figure 10).

Table 5: Analyses concerning the effect of aggregation pattern within each region. Only one mat was found and thus, not included. Average values and standard deviations for both aggregation patterns are reported with p-values denoting the results of Wilcoxon Rank-Sum Test.

Region	Test	Clump	Row	p
Caribbean	No. of indv.	83.0 ± 12.9	62.3 ± 33.3	0.145
	No. of species	3.69 ± 1.8	3.70 ± 1.3	0.984
	Clump weight (g)	39.88 ± 31.8	45.37 ± 48.8	0.908
	% Growth	15.38 ± 9.0	15.0 ±8.2	0.990
	% Decline	33.85 ± 21.9	33.68 ± 19.0	0.982
Gulf of Mexico	No. of indv.	23.93 ± 23.9	19.37 ± 13.6	0.937
	No. of species	2.65 ± 1.2	3.12 ± 1.3	0.276
	Clump weight (g)	45.63 ± 41.9	73.65 ± 44.5	**0.001**
	% Growth	30.4 ± 15.4	24.07 ± 11.8	0.070
	% Decline	39.76 ± 17.0	50.28 ± 19.4	**0.011**
Sargasso Sea	No. of indv.	19.22 ± 29.0	16.24 ± 12.4	0.174
	No. of species	2.74 ± 1.4	2.65 ± 1.2	0.951
	Clump weight (g)	23.95 ± 19.7	42.91 ± 31.9	**0.001**
	% Growth	17.32 ± 13.4	10.2 ± 4.9	**0.043**
	% Decline	26.4 ± 15.5	36.85 ± 15.9	**0.004**

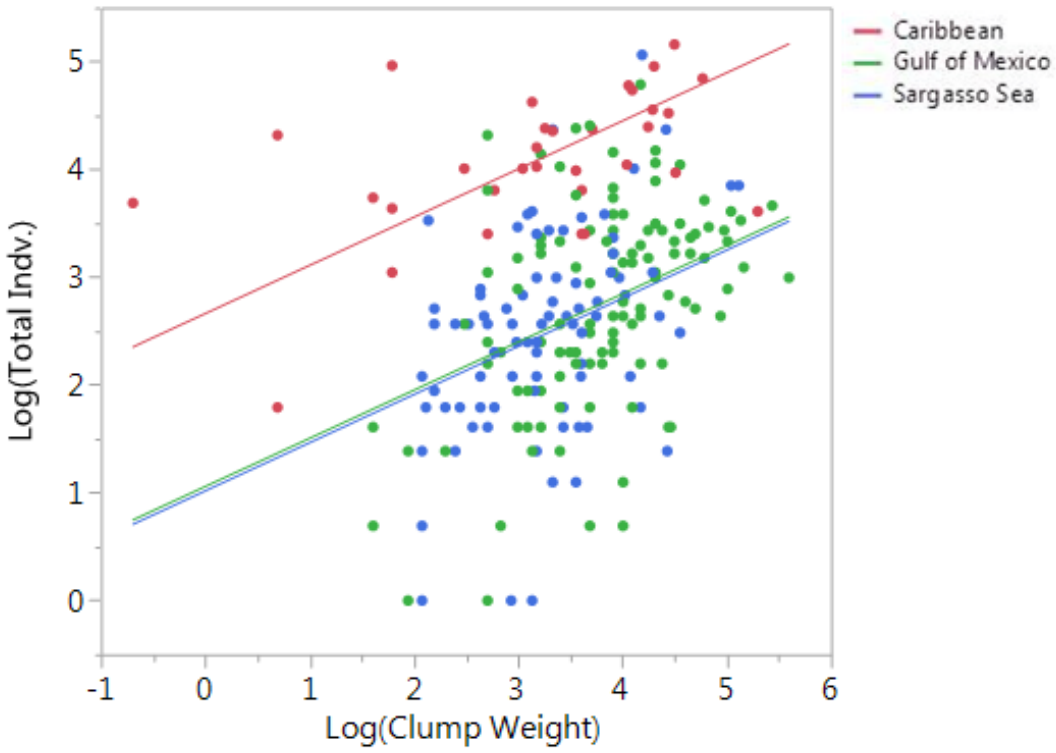

Figure 9: ANCOVA without interaction comparing the relationship between the log of average colony weight and the log of average total individuals reveals a weakly positive but significant relationship (R^2=0.38). The Caribbean supports more individuals per unit mass than the Gulf of Mexico or Sargasso Sea.

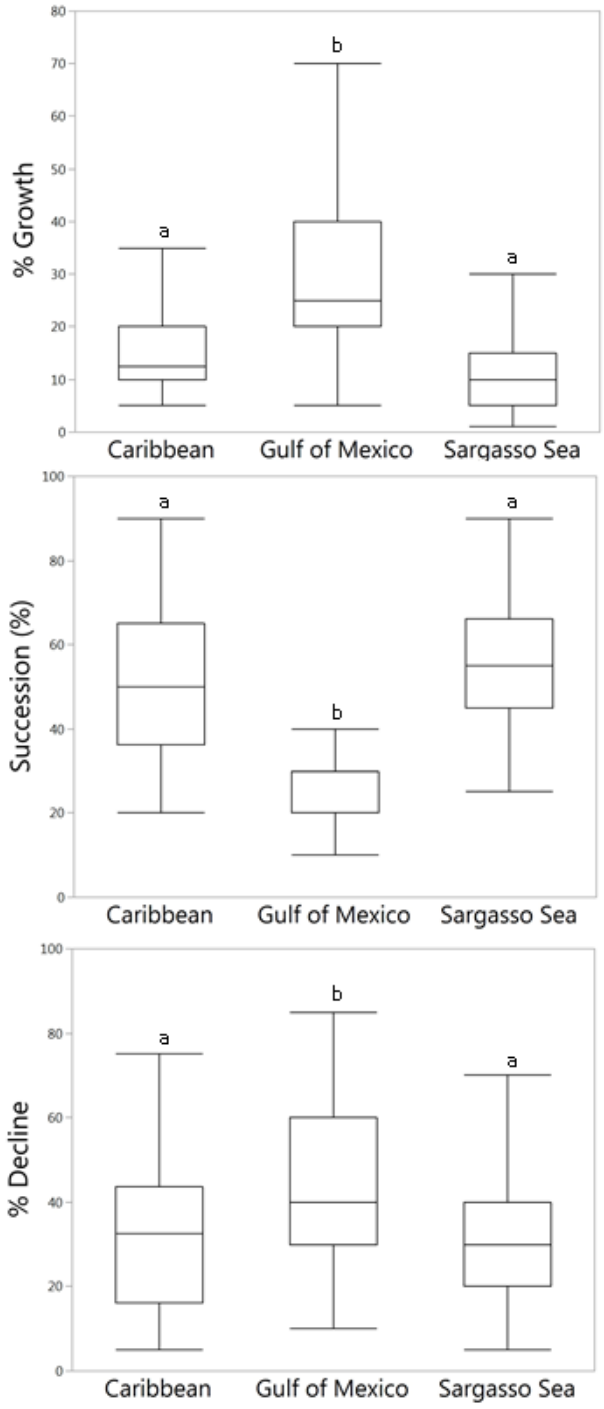

Figure 10: Significant differences ($p<0.01$, different letters indicate significant difference) in pelagic *Sargassum* colony condition (percent growth, succession, and decline) between the three regions. Box plot displays median value within 25% and 75% quantiles where whiskers denote upper and lower data points (not including outliers)

Fauna & Effect of Sargassum *Species*

A total of 22 species of fauna were observed across the three regions. The frequency of occurrence was calculated within each region and used to determine if a species was common (>10%), uncommon (<10%), or rare (<1%) (Butler et al. 1983) (Table 6). Of the twenty two species found, five were found in all three regions. The 2,722 individuals from the Gulf of Mexico were comprised of fifteen total species, nine of which were unique, and two of which were shared only with the Sargasso Sea. Weed in the Sargasso Sea contained 1,515 individuals and twelve species, five of which were unique. The Caribbean, with 2,262 individuals, had only six species, one of which was unique. No commonly occurring species were found exclusively on any one form of pelagic *Sargassum*. The commonly named slender *Sargassum* shrimp, Latreutes *fucorum,* was the most dominant species in all three regions. The Gulf of Mexico was the only region in which deliberately associated nektonic fish were found. Most flatworm species were <4mm and, because preservation had rendered them unfit for taxonomic determination, were therefore only identified to the phylum level.

Table 6: Frequency of fauna occurrence in the three regions (common >10%, uncommon <10%, rare <1%). Species shared between all three regions are in bold.

Region	Species	Taxon	Freq. (%)	Rarity
Caribbean	*Hippolyte zostericola*	crustacean	3.1	uncommon
	Flatworm spp.	**flatworm**	**31.3**	**common**
	Portunus sayi	**crustacean**	**31.3**	**common**
	Leander tenuicornis	**crustacean**	**46.9**	**common**
	Litiopa melanostoma	**mollusk**	**75**	**common**
	Latreutes fucorum	**crustacean**	**87.5**	**common**
Gulf of Mexico	*Coryphaena hippurus*	fish	0.8	rare
	Hemiramphus brasiliensis	fish	0.8	rare
	Cheilopogon melanurus	fish	1.6	uncommon
	Syngnathus pelagicus	fish	2.3	uncommon
	Abudefduf saxatilis	fish	3.1	uncommon
	Caranx crysos	fish	3.1	uncommon
	Corambella depressa	mollusk	3.9	uncommon
	Histrio histrio	fish	9.4	uncommon
	Stephanolepis hispidus	fish	13.3	common
	Flatworm spp.	**flatworm**	**14.8**	**common**
	Litiopa melanostoma	**mollusk**	**21.1**	**common**
	Leander tenuicornis	**crustacean**	**25.8**	**common**
	Portunus sayi	**crustacean**	**28.9**	**common**
	Platynereis dumerilii	Polychaete	62.5	common
	Latreutes fucorum	**crustacean**	**96.1**	**common**
Sargasso Sea	*Doto pygmaea*	mollusk	1.1	uncommon
	Anoplodactylus petiolatus	crustacean	2.3	uncommon
	Flatworm spp.	**flatworm**	**4.6**	**uncommon**
	Platynereis dumerillii	Polychaete	4.6	uncommon
	Scyllaea pelagica	mollusk	6.9	uncommon
	Histrio histrio	fish	8	uncommon
	Portunus sayi	**crustacean**	**12.6**	**common**
	Planes minutus	crustacean	20.7	common
	Hippolyte coerulescens	crustacean	29.9	common
	Leander tenuicornis	**crustacean**	**34.5**	**common**
	Litiopa melanostoma	**mollusk**	**54**	**common**
	Latreutes fucorum	**crustacean**	**89.7**	**common**

Using ANCOVA to control for the significant effect of colony weight, *S. fluitans III* and *S. natans I* support higher species richness (average number of species per colony) than *S. natans VIII* except in the Sargasso Sea where the *S. fluitans III* and *S. natans I* co-occurred (Table 7). Fauna assessments for *S. natans I* in the Caribbean were not calculated because the low sample size (n=2) was likely not an accurate representation of the region. Only in the Gulf of Mexico did the average number of individuals significantly differ between pelagic *Sargassum* forms (*S. fluitans III* – 26.9 ± 20.8, *S. natans VIII* – 16.4 ± 18.0). Community composition also varied between pelagic *Sargassum* forms. A contingency analysis of the frequencies of common fauna species reveals a significant difference between pelagic *Sargassum* forms even when accounting for variation between regions (CMH, $p<0.01$).

Table 7: Average number of individuals and species with standard deviation found per colony for each form of pelagic *Sargassum* found in the three regions. ANCOVA was used to determine significant relationships between weed species while controlling for the effects of colony weight. Where the number of *Sargassum* species exceeds two, letters indicate significant differences between species.

Region	Test	S. fluitans III	S. natans I	S. natans VIII	p
Caribbean	No. of indv.	85.4 ± 47.2		62.0 ± 30.0	0.9839
	No. of species	4.6 ± 1.3		2.8 ± 1.2	**<0.0001**
Gulf of Mexico	No. of indv.	26.9 ± 20.8		16.4 ± 18.0	**0.002**
	No. of species	3.2 ± 1.1		2.4 ± 1.1	**<0.0001**
Sargasso Sea	No. of indv.	12.7 ± 5.9	20.4 ± 26.9	11.5 ± 10.6	0.501
	No. of species	2.63 ± 0.9 [a,b]	2.8 ± 1.4 [a]	1.8 ± 1.0 [b]	**0.035**

V. DISCUSSION

Hypothesis 1

While satellite data suggests pelagic *Sargassum* follows a single path through the Gulf of Mexico and Sargasso Sea (Gower & King 2011), historical (Goodwin, Schell, & Siuda 2014) and multi-regional data suggest that this path is not entirely accurate for all forms of the algae. Using fauna diversity summary indices to compare pelagic *Sargassum* forms across each region, varying circulation patterns emerge for the three forms. Although satellite data can track pelagic *Sargassum* movements on a continuous timescale and across the entirety of its distribution, the technology is not able to detect differences in weed species nor can it detect any aggregations smaller than very large mats (Gower & King 2011), both are factors that this study has shown to result in significant effects. In this respect, the conclusions of Gower & King (2011), that pelagic *Sargassum* moves from the Gulf of Mexico to the Sargasso Sea, may not be representative of all forms. Indeed, this study suggests that none of the three common forms of pelagic *Sargassum* explicitly follow this path. Rather, the combined but distinct pathways of each form are the likely reason for Gower & King's (2011) observed cycle. Because pelagic *Sargassum* is a drifting plant and therefore incapable of independent movement, differences in apparent pathways or regional occurrences are instead likely due to a form's ability, or lack thereof, to survive in the new physical environment into which it has drifted. The following proposed annual paths of each pelagic *Sargassum* form along with seasonal diversity changes are summarized in Figure 10.

Based on field (Goodwin, Schell, & Siuda 2014) and satellite (Gower & King 2011) data, *S. fluitans III* is hypothesized to move from the Gulf of Mexico, around Florida, and into the Sargasso Sea via the Loop Current and Gulf Stream. It reaches highest abundance in the northern region of the Sargasso Sea during the fall and shifts more southerly during the spring (Figure 1). Evenness and diversity measures support this hypothesis but also suggest that in addition to moving into the Sargasso Sea, *S. fluitans III* distribution appears to also include the Caribbean. In the Gulf of Mexico, *S. fluitans III* is heavily dominated by *L. fucorum*. Outside of the Gulf of Mexico, *L. fucorum* is still the most dominant species but its frequency is reduced and other species, like *L. melanostoma* and *L. tenuicornis*, become more prevalent. While its diversity is not substantially larger in the Sargasso Sea compared to the Caribbean, its evenness is much larger suggesting that the two populations reached their destinations through different paths. This form of pelagic *Sargassum* is likely able to support a more diverse fauna community in its latter regions because of its greater succession area.

In the Sargasso Sea, *S. fluitans III* is restricted during spring to the southern region below the Sub-tropical Convergence Zone (STCZ), which is marked by a steep, decreasing temperature gradient moving north through the Atlantic (Ullman, Cornillon, & Shan 2007). This phenomenon is most pronounced during the spring in the western Atlantic, the same time and location, at which, these samples were collected. Like in previous years, *S. fluitans III* and *S. natans I* showed a sharp division in distribution at 25°N (Goodwin, Schell, & Siuda 2014). This is possibly a result of a shift in temperature and, as a result, fauna diversity, near the same latitude as the southern edge of the STCZ.

In the Caribbean, the presence of such a large quantity of pelagic *Sargassum*, especially *S. fluitans III* is particularly rare (Parr 1939). A similar pattern was only ever noted during SEA's 1992-2013 sampling period in 2011; a period of abnormal blooming similar in magnitude to 2015. Overall, these findings, in conjunction with seasonal observations of pelagic *Sargassum* distribution, suggest that *S. fluitans III* circulates from the Gulf of Mexico in the summer, up the Gulf Stream, quickly circulating into the northern Sargasso Sea in the fall, to the southern region in the spring, and, following the Antilles current through the Windward Passage, back in the Gulf the following summer. Within the Sargasso Sea, a southward shift from the fall to the spring in conjunction with decreasing SST suggests that the growth of *S. fluitans III* is temperature dependent and that it is unable to survive lower temperatures. During bloom years, it appears *S. fluitans III* is also capable of circulating further east in the North Atlantic Gyre such that it is eventually caught up in the North Equatorial Current, enabling it to enter the Caribbean.

Unlike, *S. fluitans III*, *S. natans I* appears unable to fluorish in areas outside its ideal range within the northern Sargasso Sea, above the SCTZ. Within this zone above 25°N, *S. natans I* supported the highest diversity of all *Sargassum* species in any of the three regions. This species' adaptation and ability to thrive in this particular environment are not only evident in its high levels of diversity but its high succession area as well. These findings support the original hypothesis that *S. natans I* is native to the Sargasso Sea and is rarely found outside of this region due to physiological barriers. Like *S. fluitans III*, over a twenty year period (Goodwin, Schell & Siuda 2014), *S. natans I* also exhibited a seasonal, southerly latitudinal shift within the Sargasso Sea from the fall to

spring. From these data, it appears, *S. natans I* is concurrently present with *S. fluitans III* in the northern Sargasso Sea during the fall. Both species then shift southwards until the spring, when a distributional division occurs. From there, *S. fluitans III* returns to the Gulf of Mexico while *S. natans I* is recirculated into the northern Sargasso Sea via the Gulf Stream. Like *S. fluitans III*, *S. natans I* appears to shift its area of highest density in conjunction with changing SST however, it is able to survive slightly lower temperatures. The distributional findings of *S. natans I* described as part of this study are very unlike those described by Parr (1939) who found the form dominating the Gulf of Mexico and substantially present in the Caribbean. Without continuous historical data, the cause of this dramatic shift remains unknown.

Because no specific studies concerning mobile epifauna exist for the Gulf of Mexico or Caribbean, the Sargasso Sea is the only region in which the findings of this study can be compared to historical data. Compared to fauna frequencies presented here, Butler et al (1983) found that, in the spring, nudibranchs and flatworms had much higher abundances while *L. fucorum* was comparatively rare. Stoner & Greening (1984) found that *L. fucorum* and *L. melanostoma* were the most frequently found species, however, unlike in this study, their frequencies only averaged 22% and 25% respectively. Although only qualitative in nature, Keller (1987) found that *L. melanostoma* and *P. dumerilii* occurred most frequently. Most recently, Huffard et al's (2014) comparison of pelagic *Sargassum* communities at four stations (unknown replicates) to those observed forty years prior revealed that recent samples are only 13% similar to historic samples. This was due, in part to a significant reduction in both diversity and evenness; ten

species of crustaceans and three nudibranch species were missing from recent data while eight previously unreported species were noted. These historical findings, compared with frequency measurements from this study, suggest that in the past 30 years, across multiple species of substrate, a shift has occurred in the Sargasso Sea pelagic *Sargassum* community from in which species were more evenly distributed to one now dominated by *L. fucorum*. This same dominance is present in the Gulf of Mexico and Caribbean as well but, due to a lack of historical data, no comparisons can be made.

Only ever described by Parr (1939) as marginally present in the Caribbean and Gulf of Mexico, the now unusually prevalent, once rare *S. natans VIII* displays a pattern that reflects aspects of both *S. fluitans III* and *S. natans I*. Like *S. fluitans III*, *S. natans VIII* is able to survive in multiple regions but like *S. natans I*, it appears to have an ideal region, the Caribbean, in which its relative diversity and succession area are highest. *S. natans VIII* was only found below 22.5°N, well within the boundaries of the Antilles Current or southern edge of the Sargasso Sea. When *S. natans VIII* is found in the Gulf of Mexico or Sargasso Sea, it has lower diversity and, in the case of the Gulf of Mexico, lower successional area. Contrary to the hypothesis, which postulated that *S. natans VIII* would move from the NERR to the Caribbean and into the Gulf of Mexico and Sargasso Sea, it appears that, of the three regions, it is best suited for the Caribbean although able to survive elsewhere and only exists in other regions because of strong currents. Its concurrent presence and similar diversity values in the Gulf of Mexico and southerly Sargasso Sea during the late spring/early summer suggest that the Caribbean simultaneously feeds the two regions via the Antilles and Caribbean Currents in the early

spring. Beyond these regions, it is possible that *S. natans VIII* may continue into the Gulf Stream and Sargasso Sea but its complete absence suggests it is unable to survive. It is unknown if the Caribbean is *S. natans VIII* source of origin. Although the NERR was not sampled as part of this study, it is possible that this form of pelagic *Sargassum* originated from that region and is connected with the pattern of atypical blooms. While not observed during the 2011 bloom, *S. natans VIII*'s rapid increase in abundance, from near obscurity to one of the most common forms, in addition to its apparent preference of the most southerly region, the Caribbean, suggests that it could be connected with the most recent 2015 bloom, which is thought to be sourced from the NERR. Although differences in diversity exist, with such a newly abundant species, fauna are unlikely to have developed specific affinities with the form meaning communities may still be in early stages of development.

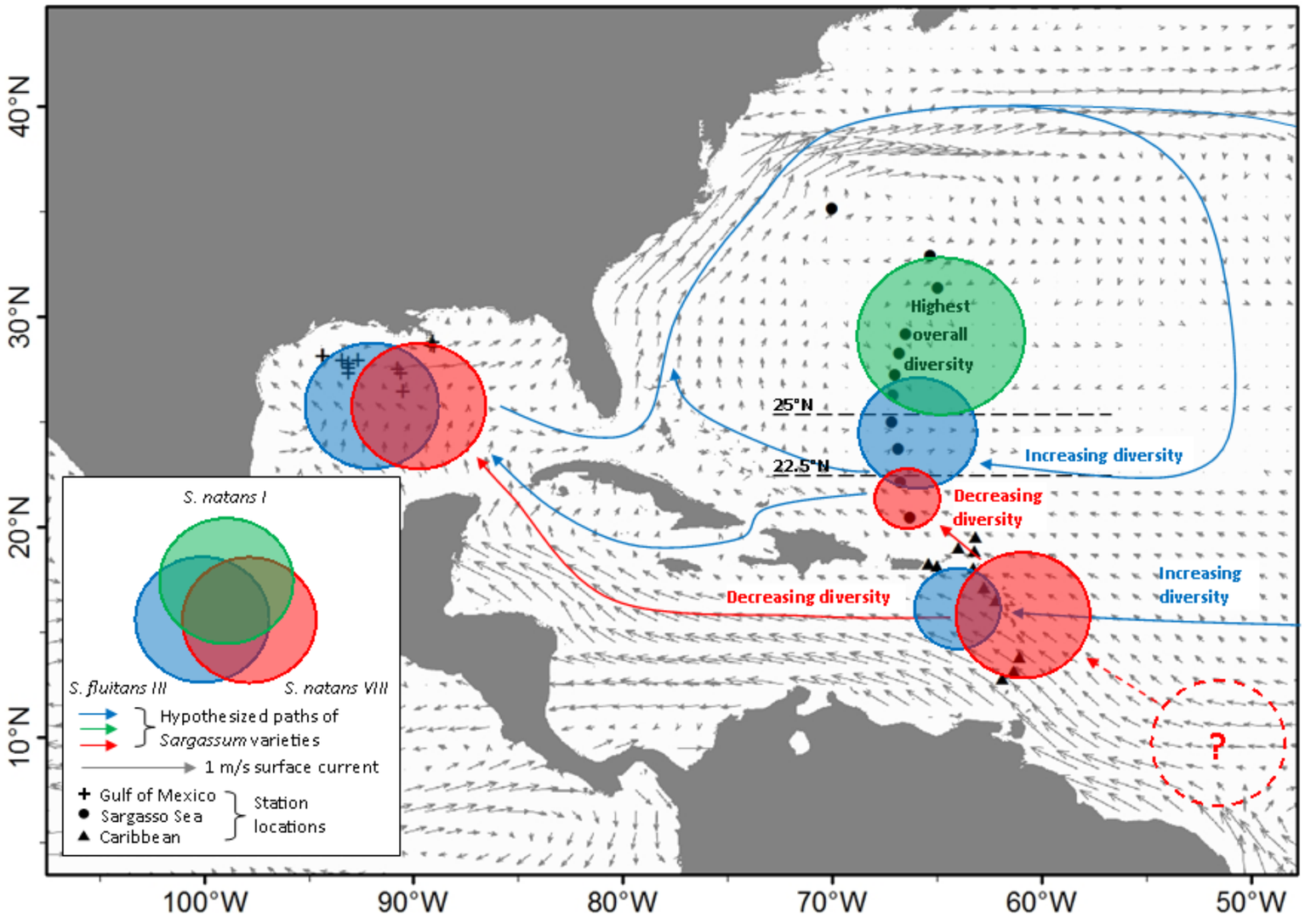

Figure 11: Hypothesized seasonal movements (arrows) of *Sargassum* using diversity as a proxy. Relative quantities of each *Sargassum* form (denoted by color) collected as part of this study are represented by variation in circle size. The extent to which each form overlaps denotes relative mixing of forms within a region. The hypothesized source region and subsequent movements of *S. natans VIII* is represented by red dashed lines. Average ocean currents during sampling period (January – June 2015) adapted from Bonjean & Lagerloef 2002.

Hypothesis 2

Despite multiple historical descriptions of the Sargasso Sea, with its mats of yellow weed as far as the eye could see, very few of these aggregation patterns were observed in any of the three regions, and only one was sampled, as part of this study. Contrary to the original hypothesis, in all regions, rows were found at higher wind speeds than isolated clumps. Based on this finding and anecdotal observations of mats and the state of pelagic *Sargassum* aggregation patterns in high sea states, a new hierarchy of patterns can be developed. In low winds, when surface currents are converging, large mats form. However, in low winds when currents are either divergent or negligible, clumps become isolated and dispersed. In moderate winds, windrows, of varying widths and levels of connectedness, are the dominant pattern. Based on observations of pelagic *Sargassum* during periods of high winds, a third level, that of scattered, isolated clumps is assumed, much like those observed by Barstow (1983). Sampling of the last pattern likely did not occur due to the difficulty of surface sampling in high wind and waves. Despite significant regional difference in wind speed, the ratio of rows to clumps did not vary.

Compared to colonies of pelagic *Sargassum* found in rows, isolated clumps had smaller areas of decline and lower weights. Under the aforementioned original hypothesis, this may have been the result of significant wave action breaking off areas of decline, which sink, causing the remainder of the colony to have less mass and smaller decline areas. Alternatively, despite the fact that isolated clumps are found at lower wind speeds, their isolation is likely the cause of a similar outcome. Although rows are found

at higher wind speeds, their larger, tangled pattern possibly prevents wave damage. Even at lower wind speeds and sea states, isolated clumps are disturbed frequently enough to cause breakage. Lower wind speeds combined with high temperatures were the likely cause of the Gulf of Mexico's greater colony mass. Collected in the spring, a period during which pelagic *Sargassum* growth is at its peak (Howard & Menzies 1969) as a result of increasing temperatures (Parr 1939, Winge 1923), regional differences in growth area were pronounced. In the Gulf of Mexico, while low wind prevents areas of decline from separating and sinking, high temperatures allow for rapid growth; the combination of these two factors results in large colonies. Despite the Sargasso Sea having a significantly lower temperature during sampling than did the Caribbean, it did not have smaller growth area. These two regions, on the other hand, did have larger succession area which could suggest that this particular age of pelagic *Sargassum* is ideal for fauna (Butler et al 1983). Stoner & Greening (1984) found evidence of community succession on pelagic *Sargassum* but had markedly different sample sizes and thus were unable to perform robust statistical analyses.

Across all three regions, the total number of individuals was weakly but significantly associated with colony mass. This positive relationship has been found previously (Butler et al 1983, Fine 1970, Stoner & Greening 1984) although no regional comparison has ever been conducted. Pelagic *Sargassum* in the Caribbean was found to support more fauna per gram of substrate than pelagic *Sargassum* in both the Gulf of Mexico and Sargasso Sea. This concentration of fauna in addition to the comparatively low mass of pelagic *Sargassum* collected from the Caribbean suggests that as substrate

moves into the region, its overall abundance is reduced, forcing more individuals onto a single colony. Across aggregation patterns, no significant differences in either species richness or total fauna abundance were noted even though colony weight differed. Butler et al (1983) postulates that this is the result of prior fragmentation of a populated colony. If emigration and immigration are low, the species richness of a colony would be decided by its initial levels. Because of the randomness associated with this type of colony formation, variation in inter-colonial species diversity is often very high (Butler et al 1983, Fine 1970, Stoner & Greening 1984) and may be high enough to swamp out a possible increase in diversity of colonies in windrows, compared to isolated clumps, when close proximity allows for limited immigration.

Hypothesis 3

Although this study was broad in its spatial scale, the composite number of species collected from all three regions represents a small fraction of known pelagic *Sargassum* mobile fauna associates. On the other hand, the nature and methodology of this study were ideal for thoroughly examining mobile and clinging fauna and provided a glimpse at juvenile associated nekton. While a dip net is ideal for conducting studies of individual substrate colonies, it is likely ineffective for capturing those species that are fast or deep enough to escape the net. As a result, most pelagic *Sargassum*-associated fish studies have utilized purse seine nets in order to analyze an entire community but, in the process, lose the ability to analyze on a smaller scale. In comparison, this study provided an excellent model of epifauna diversity and an incomplete sampling of associated fish within the pelagic *Sargassum* community, the latter of which were only

collected in the Gulf of Mexico. The proximity of Gulf of Mexico samples to broad, shallow shelf waters compared to the Caribbean's narrow shelf and Sargasso Sea's open water could explain why juvenile fish were so abundant in the region. Dooley (1972) and Settle (1993) also found a decreasing trend in fish abundance relative to distance from shore while Bortone, Hastings & Collard (1977) and Wells & Rooker (2004) found the opposite trend. These studies were conducted in shelf waters and thus their trends may not be applicable when comparing shelf (Gulf of Mexico) to offshore waters (Sargasso Sea). There may also have been a slight sampling bias when comparing the densities of highly mobile fauna, like fish, between aggregation patterns. Fish associated with isolated clumps are unable to swim to new, nearby habitat when frightened by a dip-net compared to fish living below rows where undisturbed habitat is easily accessible. Because so few fish were collected and variation, extremely high, the effect of this potential sampling error could not be tested.

While no common species were found associated with one particular form of pelagic *Sargassum*, total fauna abundance differed significantly. Similar examination of pelagic *Sargassum* species-specific association among fauna by Stoner & Greening (1984), found 22 of the 23 total species collected associated with *S. natans* and 21 associated with *S. fluitans*; inter-species fauna comparisons were not made. In this study, comparisons between *Sargassum* species showed that, as predicted, the more structurally complex *S. fluitans III* and *S. natans I* supported higher species richness than *S. natans VIII* in all three regions. *S. fluitans III* contains high order branching, numerous blades, and additional structures (spikes and thorns) creating microhabitats and more niche

spaces, allowing for higher diversity (Huffaker 1958). While significant differences were found in the Sargasso Sea, inter-regional separation of forms may introduce a spatial influence on form comparisons as compared to the Gulf of Mexico and Sargasso Sea where forms are more homogenously mixed. Total fauna abundance did not differ between substrate species or form because colony size did not vary significantly.

VI. CONCLUSIONS & FUTURE WORK

It is clear that regional oceanographic differences result in varied pelagic *Sargassum* species and form distributions and, in turn, the establishment of unique, region and species-specific fauna communities. Although they may be closely related, the most common pelagic *Sargassum* forms have distinct morphological differences which enable them to support lower or higher levels of diversity. This study is novel in its simultaneous comparison of community differences across both region and substrate form. In addition, it also demonstrates the importance of analyzing pelagic *Sargassum* at the individual colony level. Reported here, also for the first time, is fauna and substrate data concerning the newly common form, *S. natans VIII*. How the pelagic *Sargassum* community will respond to this rapid ecological shift is, as yet, unknown. The regional and form-specific differences reported in this study have implications for unbalanced negative impacts as a result of disturbances. Indeed, some change, either anthropogenic or natural, has already resulted in massive, atypical blooms as well as a long-term decrease in fauna diversity (Huffard et al 2014). Climate change and subsequent heat sequestration by the ocean (Levitus et al 2012) could impact distributions of region-specific forms of pelagic *Sargassum* and their associated fauna communities. While pelagic *Sargassum* growth may be positively associated with higher temperatures, for the northern-dwelling, site-specific *S. natans I*, a shift in temperature could drastically affect its abundance and distribution. Climate-induced changes in winds may also alter frequencies of aggregation pattern which, as this study suggests, could alter substrate decline and colony weights. Regional disturbances, like oil spills, which

disproportionately affect certain pelagic *Sargassum* species (Powers et al 2013), are likely to result in a similarly unbalanced effect on the affected species' abundance and, in turn, fauna abundance and diversity. With pelagic *Sargassum*'s drifting nature, the effects of any one disturbance are unlikely to be regionally constrained but instead, be felt throughout the Atlantic.

Although many of this study's analyses are unique, they are by no means exhaustive in this particular field. Most importantly, they have shown the necessity of identifying pelagic *Sargassum* species and form as well as conducting analyses at the individual colony scale, especially for studies concerning epifauna. In addition to the Caribbean, Gulf of Mexico, and Sargasso Sea, future studies should also include the northern Caribbean and Florida Straits to gain a more thorough understanding of form distributions. An expansive study of this nature will also give insight to the ratio of pelagic *Sargassum* that is transported between regions compared to weed that remains. The existence of regionally unique species suggests that only a portion of pelagic *Sargassum* is moved between regions. Under this assumption, species incapable of emigration can become regionally endemic however, as of yet, very little data exist to support this evolution. While associated nekton may be difficult to analyze on a colony basis, the inclusion of sessile epibionts in a similar study will allow for comparisons between fauna with sedentary lives versus those with limited immigration/emigration capabilities. Of particular importance to this area of research is the, as yet, unstudied patterns of pelagic *Sargassum* growth with respects to environmental parameters. Base-

level growth rates must be determined both by region and species before the effects of secondary parameters, like aggregation pattern and wind speed, can be determined.

While this study used indirect means to infer pelagic *Sargassum* movement on a species level, it could not provide continuous, long term data. More easily obtained satellite data, on the other hand, are able to provide continuous tracking but only at the genus level and only when aggregation patterns are sufficiently large. Future studies should, therefore, rely on a combination of these two methods in addition to scattered historical data, possibly with the addition of microsatellite tagged pelagic *Sargassum* colonies, to determine species-specific abundance and distribution patterns. Along with regional distribution, intra-regional differences in pelagic *Sargassum* species and forms should be of interest. Although the two species may be genetically distinct (Camacho et al 2015), no data exist concerning the relatedness of forms or even interspecific relatedness across populations. For an alga that reproduces through fragmentation, which could possibly result in low genetic diversity, a thorough understanding of its diversity is critical in order to predict how severely it will be affected by environmental changes. In addition to a broad spatial understanding of the pelagic *Sargassum* community, comprehensive knowledge of temporal variations, both seasonal and interannual, is vital to verify observed patterns and track long term changes. While data collected thus far hint that a significant amount of variation exists in the pelagic *Sargassum* community, in everything from substrate abundance and distribution to fauna community diversity, long term patterns have yet to be identified in the literature. Multi-season or multiyear studies

will help clarify these patterns and may enable scientists to explore contemporary pelagic *Sargassum* issues including the cause and effects of atypical blooms.

The location of the pelagic *Sargassum* community makes it extremely difficult to study over large regions or timescales but doing so is more important than ever. Pelagic *Sargassum* supports the only free-floating, self-sustaining, pelagic community in the natural world. This understudied habitat provides shelter to a number of endemic species within a flourishing community in otherwise oligotrophic waters. Dramatic changes are clearly underway with impacts reaching far beyond pelagic *Sargassum*'s surface boundaries. Now, more than ever, it is vital that a base understanding of this unique community is established so that future impacts and changes can be predicted and mediated.

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